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The Journal of HEREDITY

A monthly publication devoted to Plant Breeding Animal Breeding and Eugenics

THE GENETICS OF JACOB
R. E. Stone

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J. B. Park

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F. A. E. Crew

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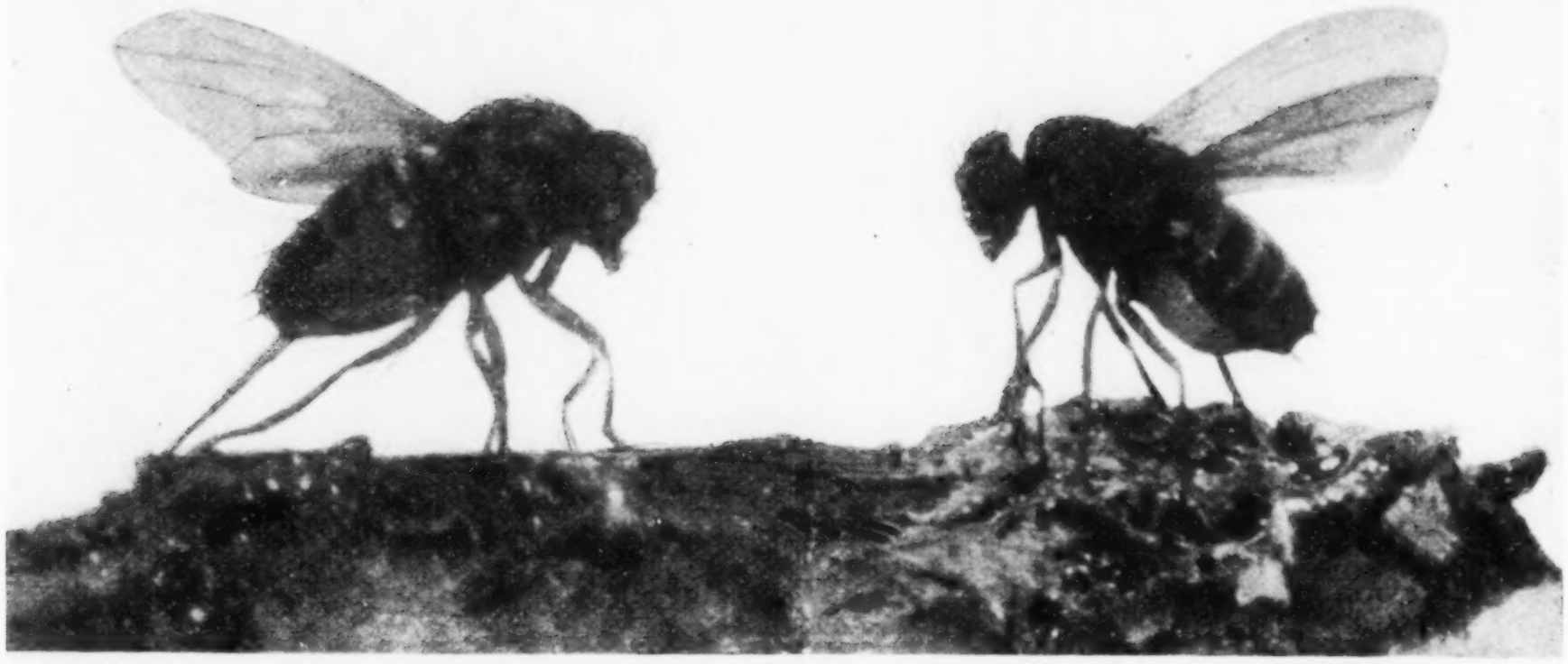
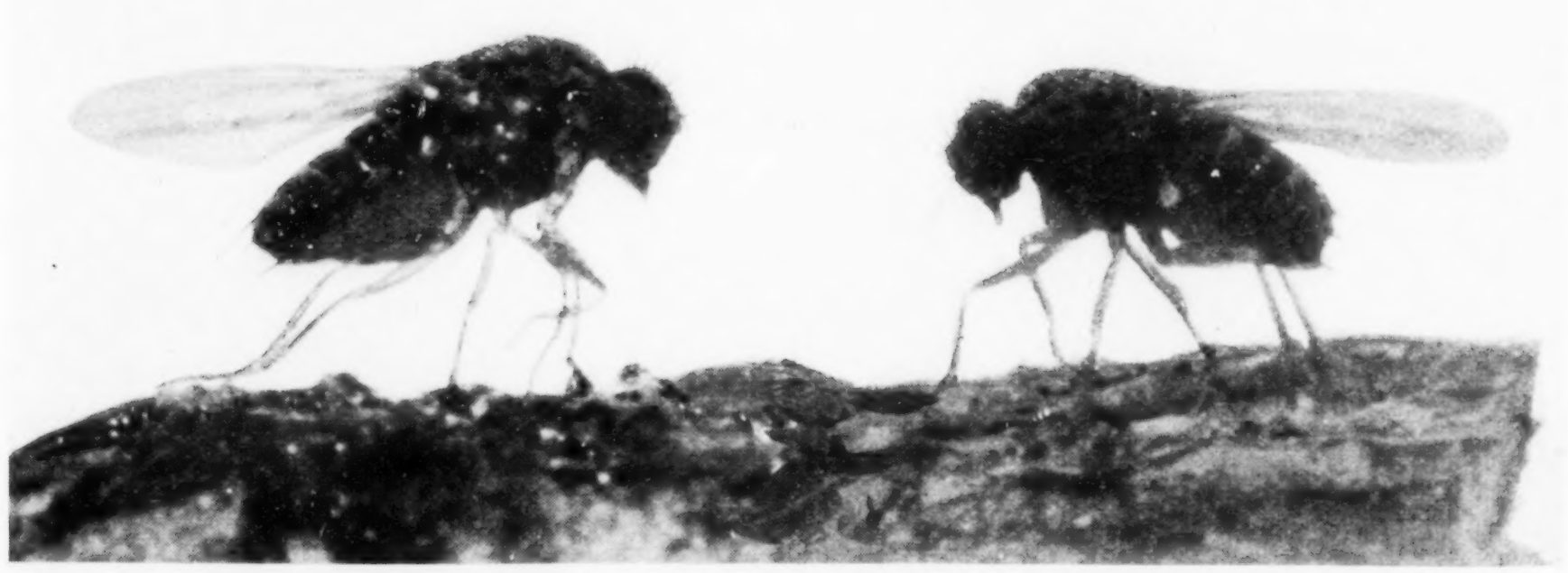




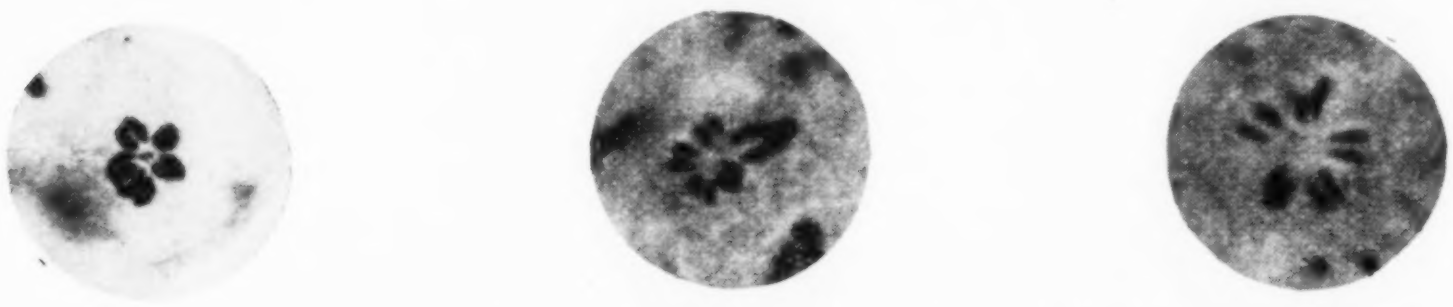
THE MULLER FRUIT FLY

More is known about the heredity of these tiny flies than of any other form of life. The ease and great rapidity with which many generations may be raised in the laboratory, and the small number of chromosomes found in the dividing cells of these flies makes them ideal subjects for studying the relation between the cell mechanism, as determined by cytologists, and the facts of heredity brought to light by genetic experiments. In this genus twelve different chromosome "patterns" are found (see Figure 2), and the attempt is now being made to discover by genetic experiments how some of these twelve types of chromosomes are related to each other. The individuality of the chromosomes within the species is well proven, and if homologies can be established between the genetic structure of these carriers of heredity in several distinct species, light will be thrown on the evolution of the chromosomes. The photographs shown above are of *Drosophila mulleri,* greatly enlarged. This species is nearly identical in external appearance with two others, *repleta* and *hydei.* In fact, no distinction was made between the three until it was found that they would not cross. Their chromosomes proved to be unlike, and minor external differences were later discovered. Photographs by Robert C. Cook. (Frontispiece.)

CHROMOSOMES OF DROSOPHILA

Chromosome Relationships and Genetic Behavior in the Genus Drosophila: I. A Comparison of the Chromosomes of Different Species of Drosophila

CHARLES W. METZ and MILDRED S. MOSES
Carnegie Institution of Washington, Department of Genetics



THE CARRIERS OF HEREDITY IN DROSOPHILA

FIGURE 1. Photographs of chromosome groups of three species of Drosophila, magnified about 1,000 diameters. The heavily stained bodies are the chromosomes, which in these flies are arranged in pairs with almost diagrammatic precision. These minute objects play the principal role in inheritance. The figures are from ovarian cells of *Drosophila virilis* (left), *Drosophila funebris* (middle), and *Drosophila ramsdeni* (right). The photographs were made from our preparations by Professor E. B. Wilson and were used by him in the Croonian Lecture of 1914, but have not been published heretofore. They are reproduced here with his kind permission.

OWING to the ease with which many species of Drosophila may be bred in the laboratory and to the fact that a wide range of chromosome groups is represented within the genus, species of this group have come to be used extensively for comparative genetical studies. The purpose of such studies is two-fold. In the first place it is desired to ascertain to what extent different species will give rise to similar mutations and whether or not similar mutant characters are inherited in a corresponding manner in the different species. In the second place it is desired to analyze the genetic make-up of the chromosomes in different species by means of linkage studies, and on the basis of such analyses to compare the chromosomes of the different species with respect to their genetic composition. In this way it may be possible to correlate the genetic structure, so to speak, of the chromosomes, with their morphological appearance, and thus to learn something of the evolution of the chromosomes.

It is our purpose to review in the present and a later paper the results obtained up to the present time. Since the selection of species for genetical study has been based, to a certain extent, upon their chromosomal relations the latter may be considered first. The present paper, therefore, deals with the cytological evidence, leaving the genetical aspects to be considered later.

In reviewing the cytological data, all of the species of Drosophila and related genera, whose chromosomes have been studied, will be included. These, of course, represent only a fraction of the known species, especially in the genus Drosophila. The descriptions are taken in large part from the previous papers, but they also include a considerable amount of new data. In presenting the data an effort has been made so to arrange them that they will

serve not only for the present purpose but also for ready reference in the future.

Description of Different Types of Chromosome Groups in the Drosophilinae

The principal known types of chromosome groups in the Drosophilinae have been described and figured in earlier papers,* [2, 3, 4, 5,] but more recent observations necessitate several corrections and changes, as well as additions to the earlier lists. It is also possible now to attach the proper specific names to some of the species not identified before, for Sturtevant has recently published a full taxonomic account of the group.[9]†

The material upon which cytological studies have been made includes twenty-seven species of Drosophila, two of Chymomyza, two of Scaptomyza, one of Mycodrosophila and one of Cladochaeta—thirty-three in all. Among these species thirteen types of chromosome groups have been found as shown diagramatically in Figure 2. All of these but one (type H) are found within the genus Drosophila. It should be stated at the outset that our cytological knowledge of some of these species is not extensive, and minor modifications may be found to separate the chromosome groups of some species now put under one type; but we believe that in all of the species included here the chromosome groups are essentially as given.

The Diptera are particularly favorable for a comparative study of this kind because of the fact that the chromosomes are arranged in pairs in an almost diagrammatic fashion in the diploid cells, somatic as well as germinal. In other words, homologous chromosomes tend to associate and remain associated throughout development. This association is indicated by the camera lucida drawings published in earlier papers (l. c.) and by the accompanying photographs (Figure 1).‡ The diagrammatic representations in Figures 2 and 4, therefore, are not as highly schematized as might be imagined. In most respects they resemble the actual figures seen under the microscope.

The thirteen types of chromosome groups (Figure 2) are not equally common among the species studied, but are for the most part represented by only one species each, with the bulk of the species falling under three main types. The distribution is indicated in the following list.

List of Species Arranged According to Chromosome Resemblance

In this list the names in parenthesis are those given in the list published in 1916[5] and subsequently changed. We are indebted to Dr. A. H. Sturtevant for the specific determination in most cases.

TYPE A

Drosophila busckii Coq.
D. bromeliae Sturt.
D. florae Sturt.
D. melanogaster Meig. (*ampelophila*)§
D. nebulosa Sturt. (*limbata*)
D. quinaria Loew.
D. robusta Sturt.
D. saltans Sturt.
D. simulans Sturt. (not in earlier list)
Chymomyza amoena Loew. (*Drosophila amoena*)
Chymomyza procnemis Will. (*Drosophila procnemis*)
Mycodrosophila dimidiata Loew. (*Drosophila dimidiata*)
Scaptomyza graminum Fall.

TYPE B

D. carlei Sturt.

TYPE C

D. calloptera Schin. (*ornatipennis*)
Scaptomyza adusta Loew.

TYPE D

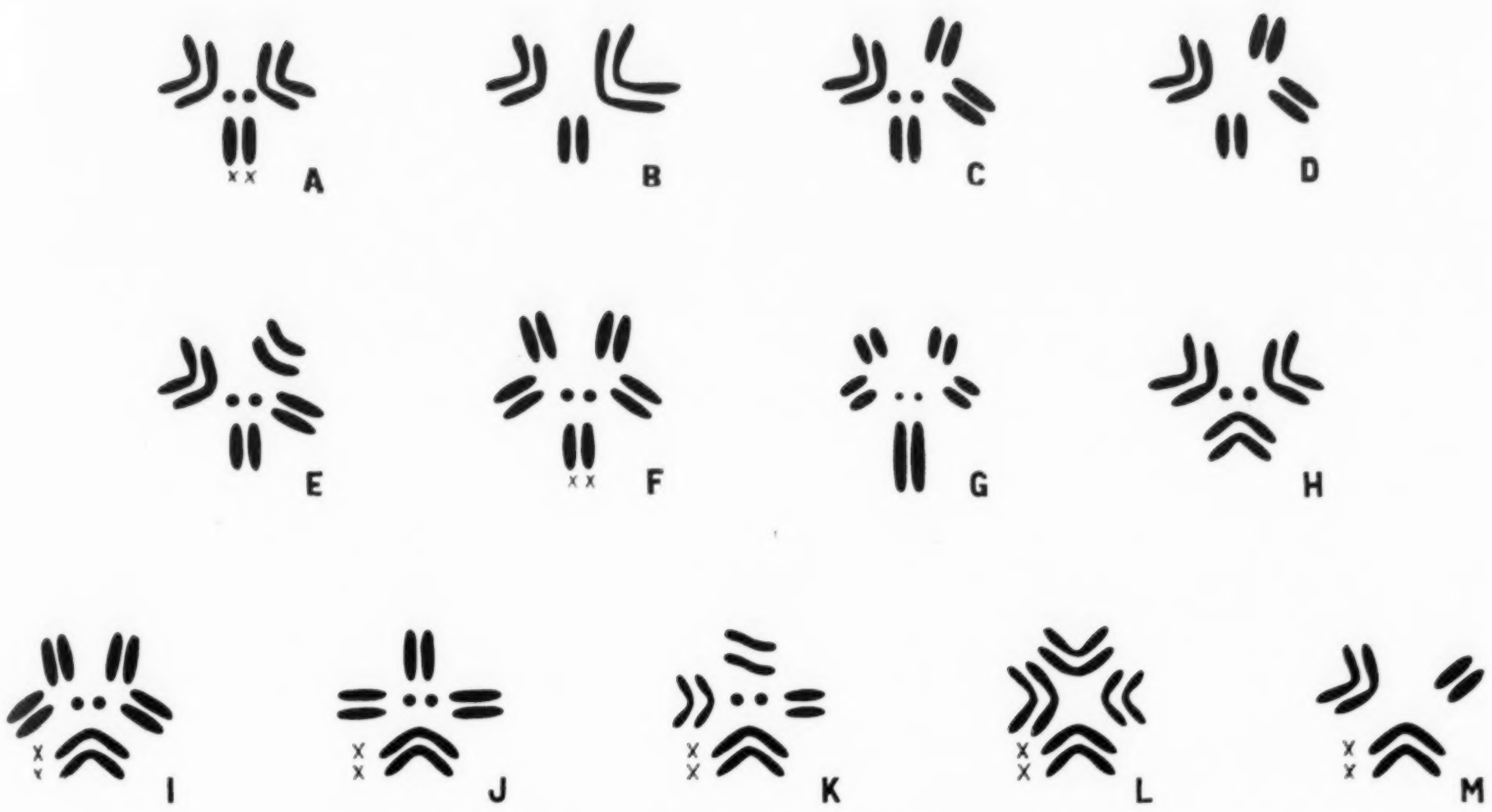
D. immigrans Sturt. (*tripunctata*)

*For Numbered References, see "Literature Cited" at end of article.

†The chromosomal characteristics are briefly reviewed in this also.

‡The drawings in Figure 3 of the present paper are from smear preparations in which the cells have been flattened and the chromosomes disarranged somewhat, hence the pairing is not so obvious.

§Names in parenthesis are those given in previous list (Metz '16b), and subsequently changed.



CHROMOSOME PATTERNS IN DROSOPHILA

FIGURE 2. Diagrams of the known types of chromosome groups in the Drosophilinae. All but Type H are found within the genus Drosophila. XX indicates sex-chromosomes. Notice the similarity between Types A, B, and M. Types A and M were confused for a time, as the absence of the dot-like chromosome may be contributed to faulty staining technique. Later it was found that the sex-chromosomes were V-shaped in M instead of rod-like as in A. The great majority of species belong in Type A or Type F.

Note: We are indebted to Miss E. M. Lord for making the drawings used in this article.

TYPE E

D. melanica Sturt.

TYPE F

D. cardini Sturt.
D. ramsdeni Sturt.
D. mulleri Sturt. (*repleta* variety a)
D. similis Will.
D. tripunctata Loew. (*modesta*)
D. virilis Sturt.
D. species? (European, resembles *D. obscura*; not in previous list)

TYPE G

D. funebris Fabr.

TYPE H

Gladochaeta nebulosa Coq.

TYPE I

D. repleta Woll. (*repleta* variety b).
D. hydei Sturt.

TYPE J

D. obscura Fall. (Oregon)

TYPE K

D. affinis Sturt.

TYPE L

D. caribbea Sturt.

TYPE M

D. willistoni Sturt. (*pallida*)

The Sex-Chromosomes

The diagrams in Figure 2 are based on the chromosome groups of the females. The sex-chromosomes here are represented by the lowermost pair of the group and are marked XX wherever they have been identified; but they have not been identified in all cases. One reason for this is that some of the species do not exhibit a conspicuous dimorphism between the X and Y chromosomes in the male (which is the criterion usually used for identification). In addition it is usually more difficult to obtain figures of the male groups than of the female groups in this material, particularly from adult flies, and consequently we lack male figures of some of the less common or less easily reared species.

The present section includes the known evidence on the sex-chromosomes and also a statement indicating where the evidence is doubtful and where it is lacking.

Sex-Chromosomes Identified

In the following species the sex-chromosomes have been identified in the manner indicated:

Type A. *Drosophila melanogaster* — dimorphism of X and Y, and non-disjunction [7, 1]; X rod-like, Y hook-shaped.

Type I. *Drosophila repleta*—dimorphism of X and Y; X long V-shaped, Y only half as long and rod-like.[5]

Type J. *Drosophila obscura* (Oregon)—X and Y as in *D. repleta*.[5]

Type K. *Drosophila affinis*—as above.[5]

Type L. *Drosophila caribbea*—as above.[5]

Type M. *Drosophila willistoni*—identified by means of non-disjunction; X and Y both long and V-shaped (Lancefield and Metz);[2] also show aberrant behavior in first spermatocyte division (unpublished data).

Sex-Chromosomes Doubtful

In a few cases our slides show indications of a sex-chromosome dimorphism, but we have insufficient material to be conclusive. These cases are as follows:

Type A. *Chymomyza amoena. Scaptomyza graminum.* In both of these it is the rod-like pair which appears in some figures to be dimorphic; but in other figures all of the pairs appear to be symmetrical, suggesting that the apparent dimorphism in the former is accidental.

Type C. *Scaptomyza adusta.* One rod-like pair appears slightly dimorphic in some figures, and appears to be aberrant in behavior in first spermatocytes.

In the case of Type F no serious problem is presented, for it seems practically certain that the dot-like chromosomes are not the sex-chromosomes and hence any one of the rod-like pairs may be assumed to be the sex-chromosomes. This is indicated alike by cytological evidence and by genetical evidence in the case of *Drosophila virilis* (to be considered later).

There remains only the species in which X and Y have not been identified, but are known to be similar, and those on which there is no evidence.

Sex-Chromosomes Apparently Similar in Male

TYPE A

D. busckii
D. bromeliae
D. robusta
D. simulans

TYPE E

D. melanica

TYPE F

D. virilis
D. species? (European, resembles *D. obscura*)

TYPE G

D. funebris

TYPE M

D. willistoni (see under first heading).

Chromosomes of Males Not Examined, or Evidence Not Satisfactory

TYPE A

D. florae
D. nebulosa
D. quinaria
D. saltans
Chymomyza procnemis
Mycodrosophila dimidiata

TYPE B

D. carlei

TYPE C

*D. caloptera**

TYPE D

D. immigrans

TYPE F

D. cardini
D. mulleri
D. ramsdeni
D. similis
D. tripunctata

TYPE H

Cladochaeta nebulosa

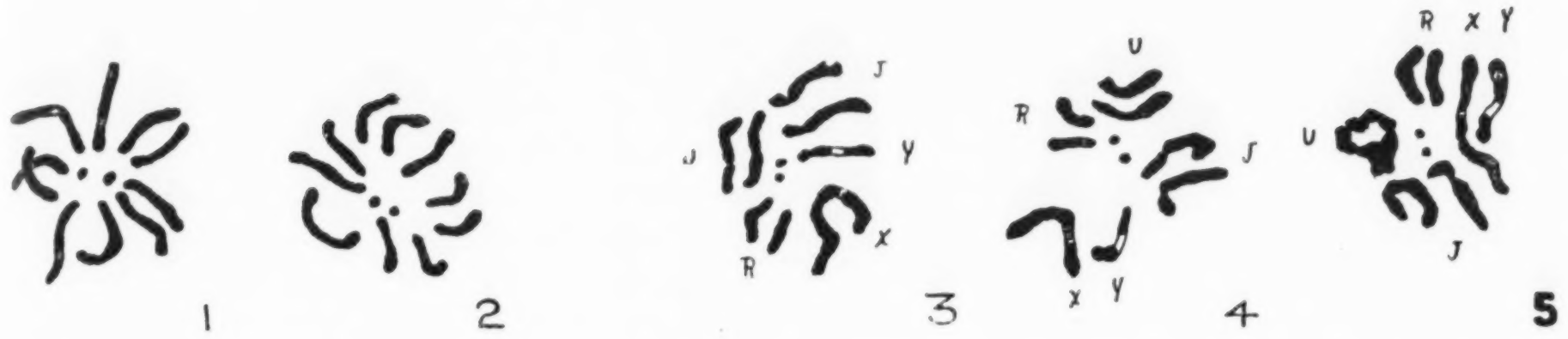
TYPE I

D. hydei.

In considering the relationships of the types outlined above it is necessary to take account of the sex-chromosome characteristics wherever possible. This necessity has recently been brought out in the case of *D. willistoni,* which was formerly included under Type A,† where the sex-chromosomes of the species used as a standard for the type (*D. melanogaster*) are rod-like. It

* In an earlier paper[5], this species (called *ornatipennis*) was erroneously said to have dimorphic sex-chromosomes.

†At that time it was not known that *willistoni* probably lacked the small dot-like pair, for only a few figures had been examined and the absence of this pair was thought to be due, possibly, to over extraction or to displacement. It will be noted that the *willistoni* group also resembles Type B, but in the latter, one V-chromosome pair is much larger than the other and the types are separated on this account.



CHROMOSOMES OF D. AFFINIS AND AN UNNAMED EUROPEAN SPECIES

FIGURE 3. Camera lucida drawings of chromosome groups from aceto-carmine "smear" preparations. Numbers 1 and 2 are from an undescribed European species of Drosophila very much life *D. obscura*. They are metaphases of spermatogonial cells and represent Type F. Numbers 3 to 10 are from *D. affinis* (Type K). 3 to 5 are from spermatogonial cells and include the full species number of chromosomes, arranged in pairs. 6 to 10 are from the second spermatocytes (which develop into spermatozoa). They include only the haploid number of chromosomes—one member from each pair. 6 to 8 represent the X-containing (or female producing) class; 9 and 10 represent the corresponding Y-containing (male producing) class. Each chromosome has its characteristic shape and size. In addition to the small dot-like chromosome (not lettered) there are the sex-chromosomes (X and Y), the small rod-like chromosomes (r), the small U- or V-shaped chromosomes (U), and the J-shaped chromosomes (J). In number 9 there appear to be two of the small m-chromosomes present, but one of these may be a granule accidentally carried into the middle of the field.

was assumed that in *willistoni* also the rod-like pair was the sex-chromosome pair, but this is not the case. By means of non-disjunction it has been shown that one of the large V-shaped pairs is the sex-chromosome pair.[2] Consequently *willistoni* has been put in a new type (M). This suggests that other species included under Type A may also possess V-shaped sex-chromosomes. And it indicates that in comparing types in which the sex chromosomes are not known it is unsafe to assume a correspondence to types in which they are known merely on the basis of general similarities between the groups.

Characteristics of Individual Chromosomes

When the individual chromosomes of the different types are compared it is seen that for the most part they fall into three main categories distinguished by size, form, and behavior. These have been described in detail in earlier papers and need only a brief characterization here, as follows:

1. *The large V-shaped chromosomes,* with median constriction and median spindle fibre attachment; oriented in metaphase with the apex of the V toward the center of the figure.

2. *The rod-like chromosomes,* approximately half the length of the V's; straight, without median constriction; with terminal spindle fiber attachment and radial arrangement in metaphase.

3. *The m-chromosomes,* small, dot-like micro-chromosomes, almost invariably in the center of the field during metaphase.

Only two of the thirteen types of groups include chromosomes that do not come under the above headings. These are types E and K. In E

there appears to be a very small V- or U-shaped chromosome pair, more or less intermediate between the rod-like and the large V-shaped kinds. Only one representative of this type is known (*D. melanica*), but we have numerous good figures of both male and female groups, including haploid (male) groups, and are able to distinguish the small U-shaped pair in nearly every case.

In type K two pairs are found which are intermediate between the V's and the rods in length. One has a subterminal spindle fibre attachment giving it an S or a hook shape. The other has a median or sub-median attachment and is much like the small V- or U-shaped pair just described in *D. melanica*. In some figures both of these pairs are somewhat S-shaped, and were so indicated in previous papers. But we have recently put up new material and have examined a series of figures which have convinced us that one pair is really different from the other. Some of these figures are represented in the accompanying camera lucida drawings (Figure 3, Nos. 3-10) taken from spermatogonia and second spermatocytes. The letters indicate respectively the X and Y (sex) chromosomes, the small rods (r), the small U- or V- shaped chromosomes (U) and the J-shaped chromosomes (J). Numbers 3, 4 and 5 are diploid groups* from spermatogonia. Numbers 6, 7 and 8 are the X-containing haploid groups of the second spermatocytes, and 9 and 10 are the corresponding Y-containing groups. In Number 9, there appear to be two m-chromosomes present, but one of these may be a granule accidently carried into the middle of the field.

Cases of what appear to be simply modifications of the V's, rods or M's are seen in types B, G, and L. In Type B one pair of V's is unusually long; in Type G one pair of rods is unusually long and the other four are unusually short, while the M's are exceptionally small (compare with Type F); and in Type L one pair of V's appears to be smaller than usual.† Otherwise the types are distinguished merely by possessing different combinations of the three main sorts of chromosomes, except where distinctions are based on sex-chromosome differences, as discussed above.

Possible Relationships Between Different Types of Chromosome Groups

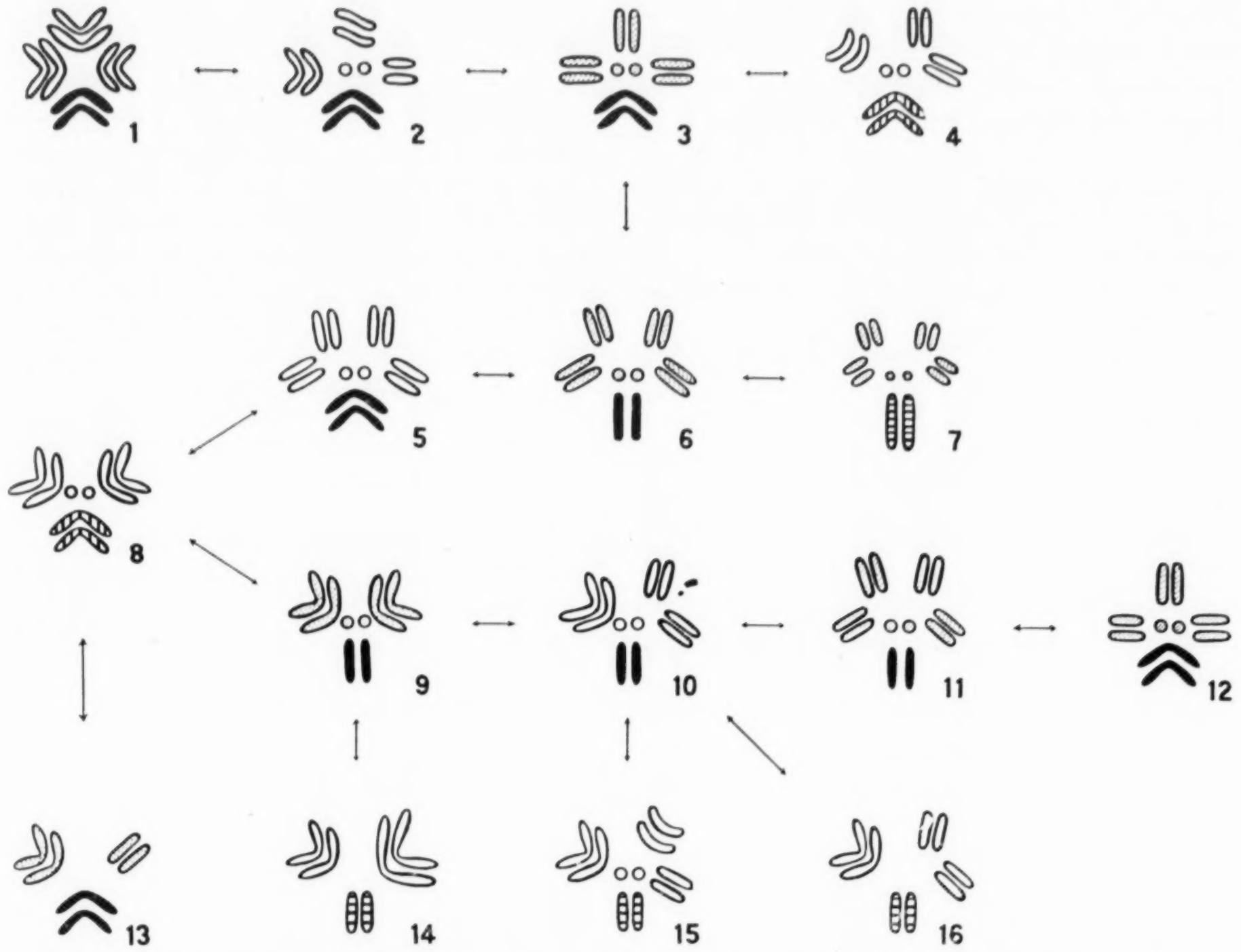
One of the most striking facts about the series of types is that many of them show such resemblances to one another that in some cases graded series may be arranged between widely divergent types. This suggests that the relationships are not purely fortuitous. It remains for genetical studies to establish these relationships, if they actually exist, but some of the possibilities suggested by the cytological findings may be outlined here.

These are represented schematically in Figure 4. In presenting this series of diagrams we wish to emphasize the fact that the arrangement is based purely on the superficial appearance of *types* and is not intended to indicate relationship between the particular *species* involved. Furthermore, it represents only one of various schemes that could be employed. It is given rather to present the problem than to indicate its solution.

In the diagrams the lowermost pair of chromosomes in each group is intended to represent the sex-chromosomes. Those given in solid black are known to be, or are believed on good evidence to be, the sex-chromosomes. The heavily banded ones are merely assumed to be the sex-chromosomes in

* In these, X and Y appear to be correspondingly segmented, as indicated by the clear band across each. This segmentation is distinct from the constriction at the point of spindle fibre attachment and its significance is not known. It seldom, if ever, appears in the second spermatocyte figures, and is presumably evident in the spermatogonia only in smear preparations.

† Perhaps this should be classed with the U-chromosomes of Types E and K, but it seems to be nearer the large V's in size.



POSSIBLE RELATIONSHIP OF THE VARIOUS CHROMOSOME GROUPS

FIGURE 4. This chart is intended only to show how the various groups may be arranged into a graded series, with the assumption of a few comparatively simple changes. These are fusion of two of the rod-like chromosomes to form a V, or vice versa, the loss of the m-pair, and changes in the size of other pairs. In order to determine whether this or any other arrangement represents the true condition, it would be necessary to study these relationships genetically. Note the similarity between the most common types shown here at 6 and 9. If the V's of number 9 were broken into rods the two types would be alike. Solid black chromosomes are known to be, or are believed on good evidence to be, the sex-chromosomes; the heavily barred ones are considered to be the sex-chromosomes in making up the series, but cytological evidence with regard to this is lacking. The stippled chromosomes indicate the types in which genetical studies are now under way that are expected to throw light on the homology of the chromosomes in the various groups.

placing the types as shown. Some types may be put in different places in the series according to whether one or another pair is assumed to be the sex-chromosome pair. This is only done in one case here, however (diagrams 4 and 15). Diagram 1 in this figure represents the most aberrant type thus far observed and is included merely for the sake of completeness. It has been found in only one species. The other types show more resemblances to one another and may be arranged in such a way as to make successive differences relatively slight. In the arrangement given here, for example, all of the differences might be accounted for on the assumption of a few comparatively simple changes. These would involve mainly the fusion of rod-like chromosomes in two's, end to end, to form V's or, *vice versa*, the breaking in two of V's to form rods, together with alterations in the size of individual pairs (particularly the m-pair) and in the form of certain pairs. The series included in diagrams 3, 6, 5, 8, 9, 10, 11 and 12 (duplicate of 3)

involves only the fusion of rods or the breaking of V's, except in the steps between 5 and 6 and between 8 and 9, where the change from a single rod to a V (or *vice versa*) is represented. The latter would involve the doubling in size of a chromosome or the diminution of a chromosome by half.

The steps involved in the other parts of the series are evident from the diagrams. One of them (10-16) involves merely the disappearance of the m-pair; another (9-14) the disappearance of this pair and the increase in size of one of the V-pairs. Diagrams 13 and 14 might equally well be put in other positions—as is true also in the case of certain others—but this would merely serve to complicate the figure.

From the standpoint of chromosome evolution several questions arise from a consideration of the above series. Foremost, perhaps, is the question as to how far morphological criteria may be relied upon as indications of genetic homology of chromosomes. This has already been answered partially, as noted above, by the observations on *Drosophila willistoni*[2] which show that in two out of three cases, at least, similar pairs are not strictly homologous when this species is compared with *D. melanogaster*[8]. However, it is possible, perhaps, to avoid the conclusion that would seem to follow from this if, as suggested above, we assume that V-chromosomes may break in two to form rods, and rods may unite to form V's. On this assumption we might start, for example, with type F and make up types A and M (the two just considered) in different ways depending on what particular rods we combined to make V's. The homologies of the rods might remain, but the resulting V's as units might not be homologous. In this case the actual relations could only be determined by genetical analysis of the chromosomes. This is one of the problems with which the actual genetical studies are concerned.

If chromosomes persist intact as hypothecated above the most definite relation between the appearance and the genetical make-up should be found in the case of the small m-chromosomes. This pair of chromosomes is present throughout almost the whole series of types, with surprising constancy of size, form and behavior. Morphological evidence is all in favor of the assumption of homology here, but again it remains for genetical evidence to furnish the proof.

Chromosome Resemblances and Taxonomic Relationships

Another question that presents itself is: What is the relation between chromosome resemblances and taxonomic affinity of the species involved in this study?

In general it is very difficult to determine the detailed taxonomic relationships within the genus Drosophila —partly because of the difficulty of deciding upon the relative importance of the various diagnostic characters. After mentioning a few aberrant forms (only one of which is included in the present paper) Sturtevant[9] (p. 70) concluded respecting the bulk of the species: "I have been unable to even make a satisfactory arbitrary division of them into groups."

In a few cases, however, two or three species show such close resemblances as to leave little question as to their taxonomic affinity, and it is of interest to note the chromosome relationships in these instances. One such case is that of *D. melanogaster* and *D. simulans*, in which the species are almost identical and may be hybridized[5]. Both of the species belong to type A with respect to their chromosomes. It has not been definitely established as yet that the rod-like chromosomes are the sex-chromosomes in *D. simulans*, but it seems safe to conclude tentatively that they are.

Another case of close resemblance is that shown by *D. repleta* and *D. mulleri*. Indeed, stocks of these species were reared in the laboratory under the same name (*repleta*) until it

CHROMOSOME DIFFERENCES IN SIMILAR SPECIES

FIGURE 5. The chromosomes of *D. mulleri* are of the F type, those of *repleta* (right) are of the I type, which differs from "F" only in having the X-chromosomes large and V-shaped instead of rod-like. Externally the two species look very much alike, and no differences were noticed until it was found that they did not hybridize. The close relationship of the two seems certain.

Figure 6. *D. obscura* has chromosomes of type J, while a similar European species has chromosomes of type F. Here the differences involve not only the sex chromosomes, but at least one pair of the others as well, for there are only five pairs in type J, and six in type F. These species do not hybridize in spite of their similarity.

was found that they differed in their chromosomes and that they would not hybridize. Subsequently they were differentiated by several external characters also, but their close relationship seems certain. One of these species (*mulleri*) possesses chromosomes of type F (one of the most common types); the other (*repleta*) is a representative of type I—which differs from F in that the X-chromosomes are long and V-shaped instead of rod-like. These relations are shown in Figure 5. Since the remainder of the chromosome group appears to be identical in the two species it might be inferred that at some time a decided change has occurred in the sex-chromosomes without visibly affecting the autosomes. If the change were from type I to type F it would seem to involve the loss of half of the X-chromosome, without necessarily affecting the Y. If it were in the opposite direction it would seem to involve the doubling of the X-chromosome.

It is of interest to note that the latter type of change has actually been observed in a mutant race of *Drosophila melanogaster* (by L. V. Morgan).[6] Here one rod-like X-chromosome has doubled leaving the two daughter elements connected end to end. This case may not have any significance in the present connection, for both sexes are asymmetrical in respect to their sex-chromosomes and half of the offspring die; but it at least demonstrates that chromosomes may become doubled and remain so.

A third example of closely related species is furnished by an American race of *Drosophila obscura* and European material of a very similar species which fails to hybridize with it.* *Drosophila obscura,* as noted above, has chromosomes of type J, while the European form falls under type F. Its chromosomes have not heretofore been described, hence we include two camera lucida drawings of spermatogonial groups in Figure 3 (Nos. 1 and 2). In both of these forms numerous good chromosome figures have been obtained and we feel confident of the accuracy of the observations. The difference here again involves the sex-chromosomes, but it also includes one pair of autosomes, as shown in Figure 6, for in F there are five pairs of autosomes and in J only four. The four are duplicated in F, but an additional rod-like pair is left over. When only the female groups are considered it might be imagined that the two X's of type J represent the two X's of F with a pair of autosomes attached at their ends; but when the male figures are reckoned with, the matter is more complicated and involves either the loss (actual or apparent) or the

* We are indebted to Dr. A. H. Sturtevant for a stock of the latter and for information about its behavior.

addition of a chromosome as large as the Y or one of the rods.

It is hardly profitable to speculate further on what has happened in the two cases just cited until genetical evidence is available, for as far as we can see, only breeding experiments will lead to the solution of the problem.

No experiments involving exactly this situation are being carried out at present, so far as we know, but there are others in progress which are sufficiently similar to give promise of suggesting the answer. In Figure 4 certain of the diagrams are emphasized by stippling. These are the types now involved in genetical studies. They include two of the types just considered—F and J. And they also include types A and M, which likewise involve differences in the sex-chromosomes. In neither of these cases are the two species concerned very close relatives, but if chromosomal homologies can be established in these cases, as seems possible from present indications, the interpretations thus provided may be applicable to other cases as well.

The above questions serve to illustrate some of the features which genetical studies are designed to clear up. A more detailed discussion will be given in connection with the genetical data.

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COLOR FACTORS IN BEAN HYBRIDS

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THE GENETIC results of bean breeding experiments which have been carried on at the Maine Agricultural Experiment Station for the past ten years are, in most cases, in accord with the results of previous investigators. Pigmentation of seed coat is dependent on a factor P, the recessive of which results in white beans. Mottling has been attributed to two factors in the same linkage group, both of which are necessary to produce mottling. Either mottling factor may exist independently in uniformly pigmented beans and when brought together by such parents result in mottled beans which do not breed true. However, some rather unusual results have been obtained with eyed beans.

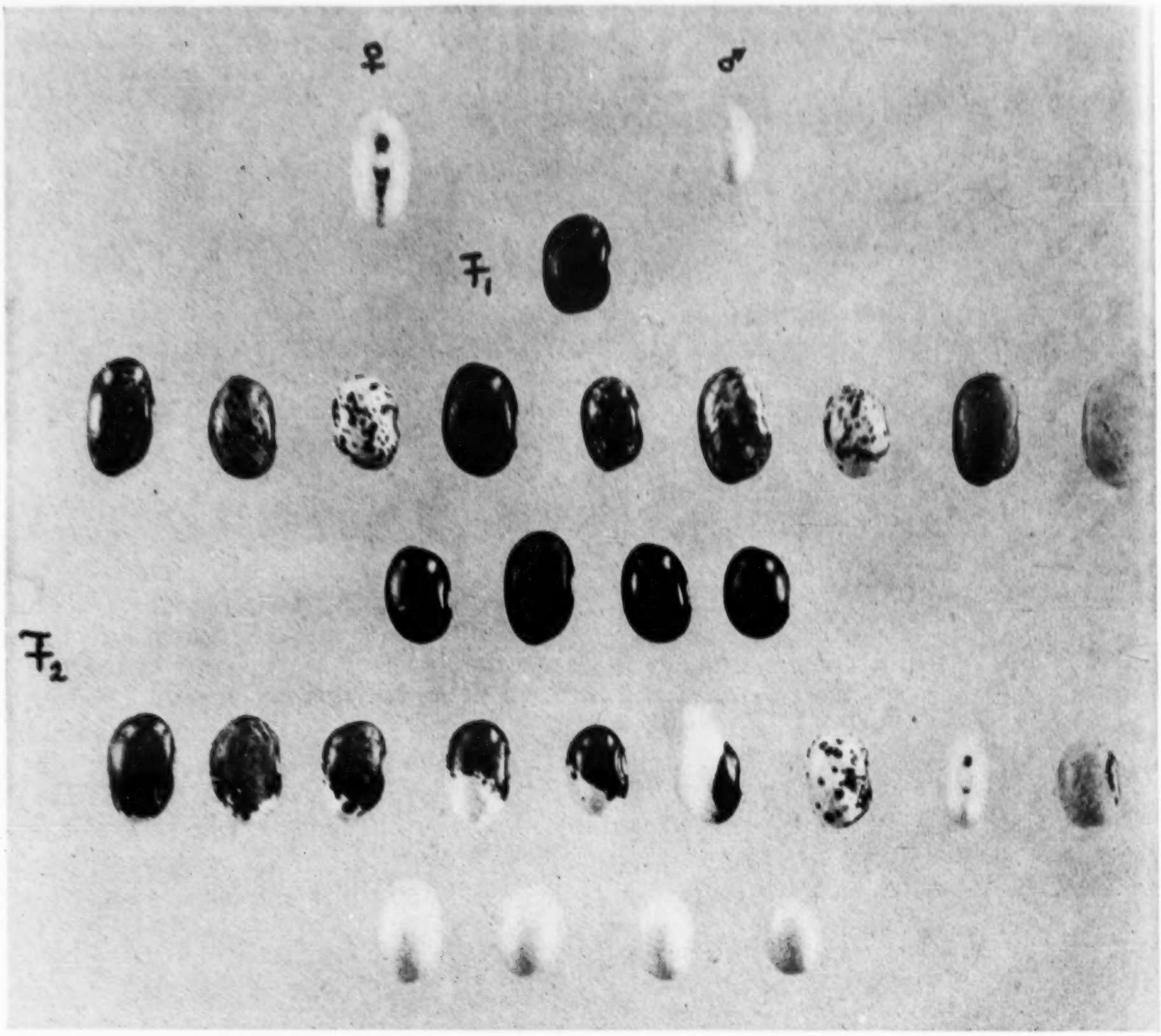
The behavior of certain crosses of eyed beans is of considerable interest in regard to allelomorphic relationships. The parents used are known under the rather local names of Old Fashioned Yellow Eye (*O. F. Y. E.*) and Improved Yellow Eye (*I. Y. E.*) The type of eye pattern of each variety is well illustrated in Figure 8. In the *O. F. Y. E.* the pigmented area covers about one-sixth of the surface of the seed, while in the *I. Y. E.* about one-fourth of the bean is pigmented.

The cross *O. F. Y. E.* × *I. Y. E.* results in "Piebald" beans in the first generation which have over twice as much pigmented surface as is found in either parent. This type of eye is irregular in outline and is accompanied by circular areas of pigment on the side of the bean opposite the hilum. In the second generation the segregation is 1 *O. F. Y. E.*: 2 "piebald": 1 *I. Y. E.*, indicating that only a single pair of allelomorphic factors are involved. The actual second generation segregates gave approximately 1:2:1 ratios, but in order to get larger numbers the second generation "piebald" beans were carried to the third generation. The behavior of these third generation segregates is shown in Table 1.

Each second generation "piebald" segregate was planted separately and in every case their progeny in the third hybrid generation segregated into *I. Y. E.*, *O. F. Y. E.*, and "piebald." The numbers of segregates in each class is a very good fit for a 1:2:1 ratio as indicated by the probable errors. The test for goodness of fit gave a value of P = .8.

The "piebald" character is rather variable, but seeds from the same plant are just as variable in pattern as seeds from different plants. In some cases the pigment is extended over almost the entire bean so that less than ten per cent of the seed coat is white. In no case did the piebald segregates breed true. The eye pattern of the eyed segregates varied somewhat in the second and third generations, but there was no difficulty in classing the segregates as *O. F. Y. E.* or *I. Y. E.* Over 300 such parental segregates were planted and not one failed to breed true.

It is evident that only a single pair of allelomorphic factors are involved in this cross. When these factors are in the heterozygous condition the pigmented area is more than doubled as compared with the parents and the eye pattern is not intermediate nor does it resemble the pattern of either parent. Usually a single pair of allelomorphic



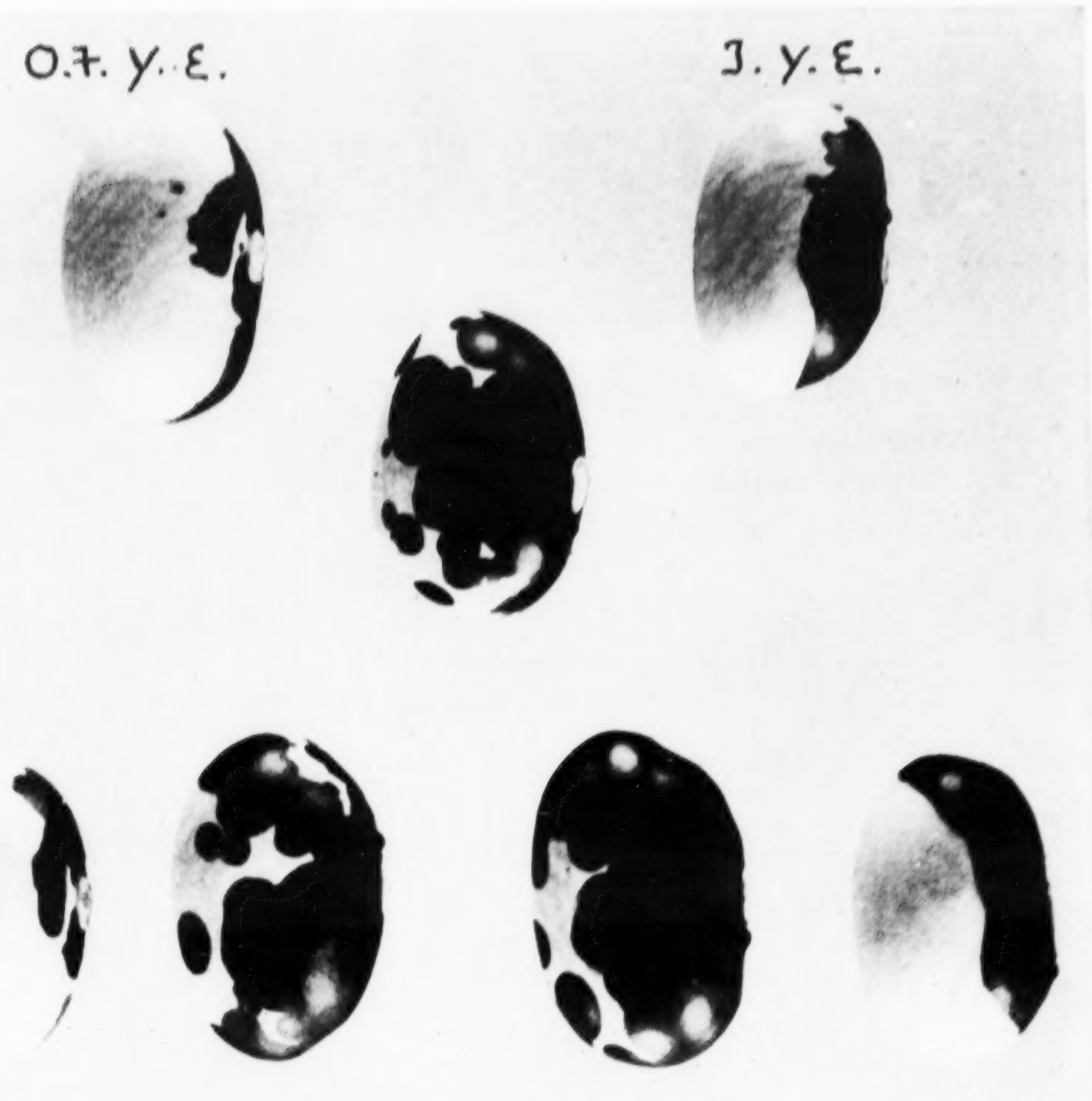
THE RESULT OF CROSSING EYED BEANS WITH WHITE

Figure 7. The first generation is dark mottled, and in the second are found mottled, solid colored, eyed, and white beans. The fact that crossing two light colored strains produces such dark beans is accounted for by assuming that the white parent carries an "Extension factor" that spreads the pigment, confined in the eyed parent to the region of the hilum, over the entire seed. Two or more extension factors may act with different colors of pigment, so that various patterns, with mottled or solid color backgrounds, occur. Photograph by C. H. White.

factors result in a character intermediate between the parents or resembling one parent or the other. In this cross of the eyed beans the factors in a heterozygous condition not only cause a great increase in area or amount of pigmentation but also cause an entirely new eye pattern.

Eyed and White Beans

Crosses of eyed beans with white beans have given various types of segregation in the second generation. In the cross *I. Y. E.* × White 1333, the first generation was dark mottled and the second generation gave a ratio of 27 mottled: 9 solid: 12 eyed: 16 white. When two extension factors are present one factor may extend one class of pigments while the other extends another pigment, so that we may get an eye pattern on a solid or mottled background. This type of pattern is shown in the last bean of the eyed series in Figure 7. Usually the eye is yellow or black while the



CROSSING EYED BEANS

FIGURE 8. The cross, Old-Fashioned Yellow Eye × Improved Yellow Eye, results in "piebald" beans in the first hybrid generation which have over twice as much pigmented area as either parent. The second generation ratio is 1 *O. F. Y. E.*: 2 piebald: 1 *I. Y. E.* The two alellomorphic factors for eye pattern when heterozygous cause a greatly increased extention of pigment, and an entirely new eye pattern. Photograph by C. H. White.

background is grey or light purple. The eye may be very definite in outline as in the *I. Y. E.*, or it may blend gradually into the white or pigmented background.

The great variability of the second generation segregates in crosses of eyed with white beans is shown in Figure 7. The color of pigment includes black, brown, yellow, purple, and red with a large series of intermediate shades. Numerous types of mottling are also found. The mottled pattern may consist of small irregular patches on a pigmented background or the background may be white. Often several mottling patterns are superimposed on one another. The patches of pigmented area may be of various shapes and sizes. In some cases the mottling pattern is associated with sunken areas of the seed coat. The uniformly pigmented beans also show great variability in color of pigment. In the second generation a large series of eye patterns are obtained ranging from individuals with more than ninety per cent of the seed coat pigmented to segregates which have only a small dot of pigment at one end of the hilum. In crosses of *I .Y. E.* × White involving several thousand second generation segregates the *I. Y. E.* parental type, in respect to size, pattern, and color, was rarely if ever recovered.

It is also found that factors for seed weight are associated with factors for

pigmentation, eye pattern, and extension factors. In all crosses of large eyed beans with small white beans the pigmented segregates in the second generation had a greater average seed weight than did the white segregates, It is estimated that about five or six size factors must be involved in most of the crosses studied. These size factors are independent in their effect and since they are often closely linked with factors for qualitative differences the effect of single factor differences for size can be studied.

TABLE 1. *Progeny of F_2 "Piebald" segregates*

Phenotype	*Observed No.*	*Observed Ratio*	*Theoretical Ratio*	*Probable Error*
Piebald	805	2.02	2	± 0.03
I. Y. E.	386	0.97	1	± 0.03
O. F. Y. E.	402	1.01	1	± 0.03
Totals	1593	4.00	4	

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FURTHER DATA ON WEBBED TOES

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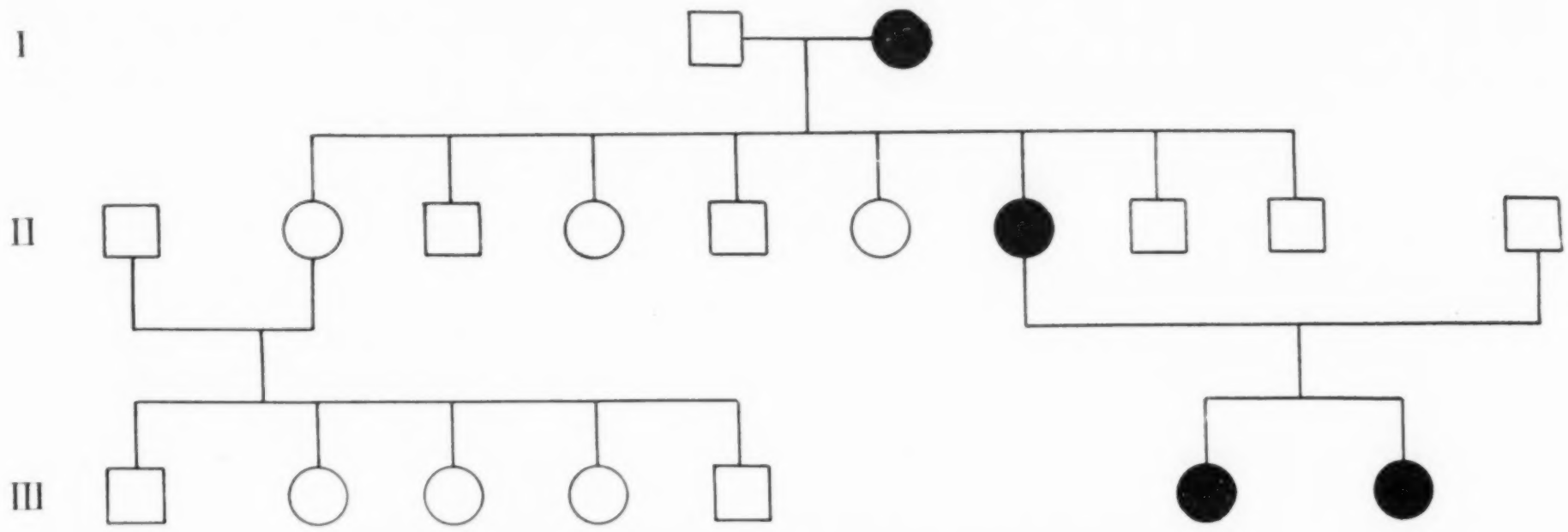

WEBBED TOES IN FEMALE LINE ONLY

Figure 9. Considerable data have been presented previously in the Journal of Heredity on the inheritance of this character. In one case webbed toes appeared only in the male line, in all the rest of the families, both sexes were affected. In this family only the women have webbed toes, suggesting that the character is carried in the Y-chromosome.

THE INHERITANCE of webbed toes has been discussed in the Journal of Heredity by Hurlin,[1]* Schofield,[2] Schultz,[3] and Wright[4] and six different pedigrees bearing on the matter have been presented. A seventh pedigree has been sent in by a correspondent who points out that it does not accord with the interpretation of Y-chromosome inheritance suggested by Schofield's data.[5] In this, a Delaware family, the character has been observed in females only and is traced through three generations, involving four individuals (See Figure 9). It is noteworthy that there were three unaffected sisters as well as four unaffected brothers of the affected individual in generation II. The idea that the Y-chromosome may be the vehicle of transmission of the character suggested in connection with the Schofield pedigree is clearly not applicable to this family, but this case could be brought into harmony with that interpretation if we suppose that in man, as in certain fishes[6, 7, 8] either the X or the Y chromosome may be the vehicle of transmission, and genes may cross over from X to Y or *vice versa*. In this family obviously the X-chromosome would be a suitable vehicle, whereas in the Schofield family, the Y-chromosome alone would meet the requirements.

But if we extend the inquiry to other pedigrees reported by Hurlin, Schultz, and Wright, difficulties are encountered. Considering together all the seven pedigrees, sixty-five cases of transmission from parent to child are reported. The transmission is from father to son in forty-one cases, from father to daughter in seventeen cases, from mother to son in three cases, and from mother to daughter in four cases. Aside from the fact that the character is more often reported in males than in females, there is no reason to think that the character is either sex-linked or sex-limited. It is a simpler hypothesis to suppose that the character depends on the transmission of a dominant gene

*For Numbered References, see "Literature Cited" at end of article.

located in one of the ordinary chromosomes than to refer it to a gene located either in a Y or an X-chromosome. However, the Schofield genealogy, if correctly reported, suggests very strongly Y-chromosome transmission, since the character here passes from father to son, but not from father to daughter, nor through the daughter to the grandsons, as in X-chromosome transmission. If the Schofield genealogy has been correctly reported, I concur in the view expressed by Wright that the vehicle of transmission is not the same there as in the other families mentioned.

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World's Dairy Congress To Meet

Great emphasis will be placed upon the possibility of improving dairy herds and increasing milk production by the careful selection of breeding stock and the gradual elimination of inefficient animals at the World's Dairy Congress. The sessions will be held at Washington, D. C., on October 2 and 3; at Philadelphia, Pa., on October 4, and at Syracuse, N. Y., from October 5 to 10.

The program is being designed broadly for four great groups and the topics of discussion have been arranged under the headings: I, Research and Education; II, Industry and Economics; III, Regulation and Control, and IV, National Health. The chairman of the Program Committee is Dr. L. A. Rogers, Director, Research Laboratories, Dairy Division, United States Department of Agriculture. Members of a Program Advisory Committee have been appointed by such national organizations as the breeders' associations, the Red Cross and the American Child Health Association.

About 200 papers have been prepared, about half by delegates from other countries. Most of these will be presented at Syracuse, where five sessions will be held simultaneously each morning. Two entire sessions will be devoted to breeding, heredity, efficiency and kindred topics. Among the papers will be: "The Wisconsin Experiment in Crossbreeding," by L. J. Cole; "The Inheritance of Milk Production and Butterfat Percentages," by J. W. Gowen; "The Development of the Dairy Shorthorn in England," by Major G. J. Buxton; "Measures Found Effective in Raising the Productivity of Danish Dairy Cows," by Lars Frederikson; "Relations Between Quantity and Availability of Calcium in the Ration and Yield of Milk Cows," by E. B. Meigs; "Some Aspects of the Physiology of Milk Glands," by Haakon Isaachsen, of Norway; "The Relation Between Nutrition and the Productive Function," by E. M. Evans. Among the speakers at these and other sessions will be: E. V. McCollum, of Johns Hopkins University; H. C. Sherman, of Columbia University; L. B. Mendel, of Yale University; Robert Burri, of Switzerland; R. H. Leitch, of Scotland; Willibald Winkler, of Austria; Osakar Laxa, of Bohemia; A. Miyawaki, of Japan, and Charles Porcher, of France.

THE HUMAN CONSTITUTION

A REVIEW

ANCIENT and medieval physicians were wont to classify mankind according to temperament—sanguine, melancholic, lymphatic, phlegmatic, bilious, and the like. With the progress of science, these more or less mystical categories were abandoned, and attention devoted to the detailed characteristics of the individual.

From this point of view it is evident that a man is merely the sum total of all his traits and characteristics. But as his characters are correlated with each other to some extent, it is not inconceivable that they might be so grouped as to justify the formation of classes of constitution, replacing the "temperaments" of older writers.

In the United States, little attention has been paid to the constitution, in this sense of the word, but during the last decade or two it has had a number of energetic students in Europe—Germany even has a *Zeitschrift fuer Konstitutions-Lehre* (Journal of the Constitution). Numerous books have been written on the subject, and one[1] of the latest of these, by Hans Gunther, furnishes a convenient opportunity to examine the ideas on which this study is based.

In the author's definition, the constitution is "the *organization* of the sum of the inner factors that make up a living organism" This, as the author admits, is abstract enough; it might lead to nothing more than a study of genetics, and the author, in fact, proceeds to discuss heredity and variation along conventional lines. He then describes the "norm," but as there are three different and equally valid norms (the mean, mode and median) it is practically impossible to establish any standard constitution for the human race, unless some arbitrary assumptions are made.

Here the author is obliged to admit that "We will never be able to grasp in its entirety the complicated structure of the constitution of an organism. Only individual characteristics, simple traits of character-complexes, are accessible." This might be thought to dispose of the need of any further study of the constitution as such. Instead, Dr. Gunther introduces a whole flock of "partial constitutions." In addition to the individual constitution there is the familial constitution, that of the local race, the race, and the species; on the other hand, there is the psychic constitution, the professional constitution, the clinical-sematic type, and so on. Again, the masculine constitution must be differentiated from the feminine; the latter, according to Aschner, is distinguished by the following characteristics:

"1. Less tension of the ligaments (hence enteroptosis is found as an anomoly in at least 30% of all women.

"2. Greater resemblance to the character of the child and greater tendency to infantilism.

"3. Greater irritability of the nervous system (tendency to hysteria and sensitivism, more intense and widespread erogenous zones).

"4. Quicker and richer production of blood and other fluids (tendency to congestion)."

Another classification, all too reminiscent of the "temperaments" of Hippocrates and Galen, is that of Sigaud and the French school, based on bodily form, which divides mankind into four

[1] *Die Grundlagen der Biologischen Konstitutionslehre*, by DR. HANS GUNTHER, Privatdozent fur innere Medizin an der Universitat Leipzig. Pp. 136, 22 illustrations. Price, $0.65. Leipzig. Verlag von Georg Thieme, 1922.

types—the cerebral, respiratory, muscular and digestive. These are said to be hereditary, and so constant that they are distinguishable even among nurslings. Naturally, intermediate forms are also to be found; cerebro-muscular, and so on. It has been stated that the French military authorities make use of this classification for some purpose.

Numerous other classifications are proposed; the hypothenic (asthenic) contrasted with the hypersthenic, for example, and perhaps a dozen others of similar style and, it would seem, similar limitations.

Several chapters are devoted to diseases and abnormalities, and much information about human heredity is introduced; indeed, the somewhat bald outline of this review does not adequately suggest the large amount of information that Dr. Gunther has packed into his scheme. Several novelties are brought in; thus the author holds that when a recessive character (albinism, for instance) appears in a pedigree, the cases are not distributed haphazard but are governed by a rhythm which will result in, let us say, every third child being affected. This is inherently improbable, and would require more abundant proof than Dr. Gunther gives.

A bibliography of nearly a hundred titles shows that the study of the constitution does not lack exponents in modern Germany. Dr. Gunther's book, despite numerous points of excellence, does not seem to the reviewer to justify such a study. So far as theory is concerned, the attempt to embrace all human traits in a given constitution is likely to lead only to confusion and mysticism. And in practice the first thing that is done is to forget about the constitution and deal directly with the individual traits. To establish enough correlations among these traits to justify dealing with constitutions would require (assuming that it is possible at all) exhaustive statistical work, which has not yet been done. Much of the trustworthy research in this field has been unfavorable—the correlations expected on the basis of popular beliefs were found to be absent. To take a simple example, it has been shown that there is not a close relation between high intelligence and large skulls. At present the "Konstitutionslehre" appears, at the very best, to be well ahead of its time.

PAUL POPENOE.

The Care of the Child

HEREDITY AND CHILD CULTURE, by HENRY DWIGHT CHAPIN, M. D., with a foreward by Professor Henry Fairfield Osborn. Pp. 219. Price $2.50. New York, E. P. Dutton & Co. 1922.

To trace, in a practical handbook for parents, the outlines of genetics and their relations to the training of the child, is a task well worth while. Dr. Chapin has undertaken it, but is not qualified to succeed in it because of lack of knowledge and lack of sympathy with eugenics. Having set out to deal with heredity, he naturally has to drag the subject in, and in a few early chapters gives an undigested mass of quotations, some facts, and some misstatements of fact; but by the time he reaches his last chapter, on the adoption of children, he has apparently forgotten all he ever knew about heredity. The bulk of the book is made up of the kind of material on the care of children, which appears in all other handbooks for parents. P. P.

SELECTION IN BROOM CORN[1]

J. B. PARK

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THE market value of broom corn is greatly influenced by the quality of the brush. Good heads should have long, slender, round fiber and be as free as possible from crooked, twisted, and kinky brush and from central stem. Brush having these undesirable characteristics is sorted out and sells at a very low price. Every crop contains a greater or less amount of this low grade product.

The opinion is common among growers that quality in broom corn is entirely controlled by seasonal conditions and that the kind of seed planted makes very little difference. Accordingly many growers use the most careless methods of securing seed, some even using seed from the broom corn thrasher where all kinds and qualities of brush are thrashed and the seed mixed.

The literature of broom corn improvement is meager indeed. Rothgeb[2] working in Oklahoma, found that varieties differ in productiveness, and that the differences are most pronounced in unfavorable seasons. He states that seed from commercial sources is likely to be of poor quality and he believes that strains which produce a more uniform quality of brush can be developed by selection of desirable seed heads. He states further that environing conditions influence the length and quality of the brush, thick stands tending to produce short brush and thin stands long coarse brush.

Central stem is illustrated in Figure 11. It is an extension of the rachis, varying greatly in length and thickness. Some stemmy heads are entirely worthless. From others the stem may be broken out by the broom-maker leaving the rest of the head of fairly good quality, but this involves labor and waste of material. If a strain could be produced which contained no central stem or a smaller proportion of it, the cash value of the crop would be greatly increased.

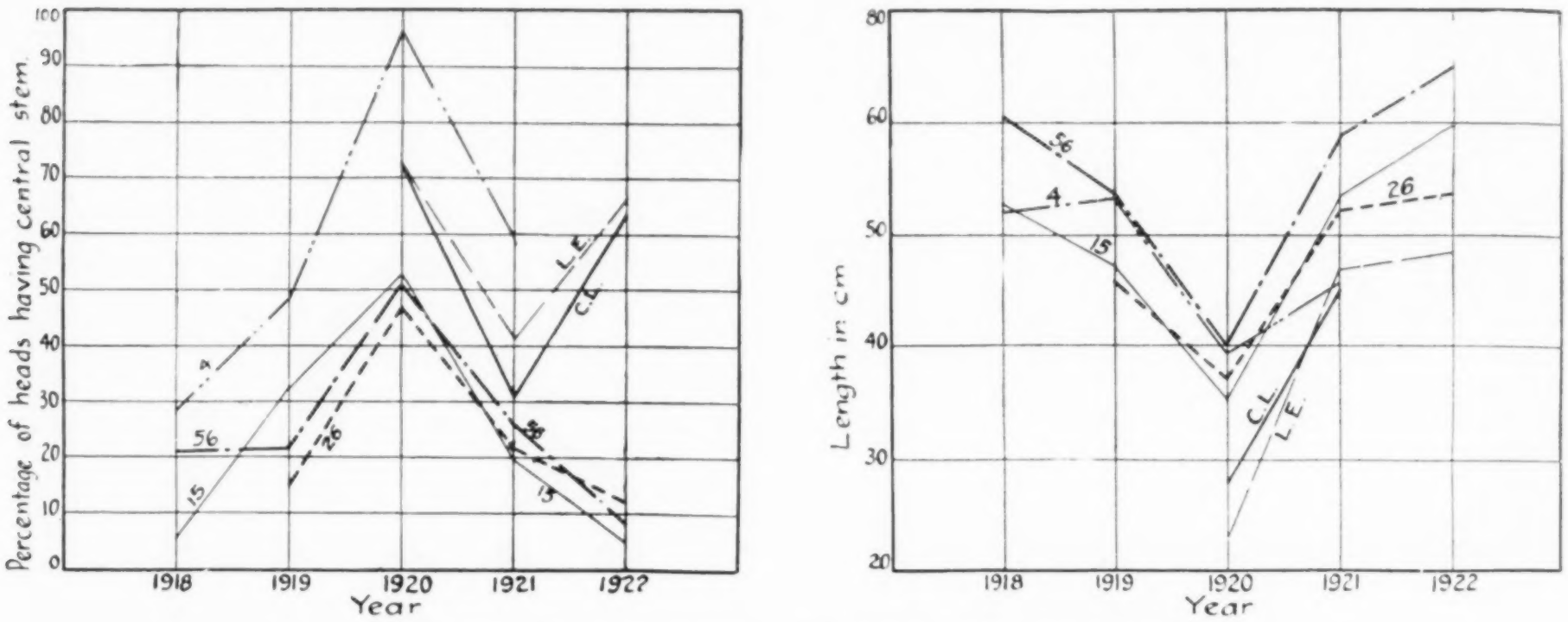
The experiment reported in the present paper was undertaken to show whether or not central stem is an inherited character and whether it can be reduced in amount or possibly eliminated by selection. Work was begun in 1917 by planting about one-tenth acre to the variety Longbush Evergreen from seed bought of an eastern seedsman. In the fall, 105 heads of good quality were selected from the crop and these were planted in the spring of 1918 in head-rows about thirty feet long. In the fall of 1918 a few of the best quality rows and some other typical ones were chosen, the brush was harvested and statistical measurements recorded for length of brush, degree of fineness, amount of kinky brush, and of central stem.

These first head-row populations, grown from open pollinated seed, showed in many cases a decided family resemblance within the head-row and conspicuous differences between rows. See Table 1.

For example, strain 56 is characterized by a moderately fine fiber. Strain 46 has short brush with a high percentage of the heads containing central stems.

[1] Contribution from the Department of Farm Crops, Ohio State University, Columbus, O. The author desires to acknowledge the assistance of Messrs. L. E. THATCHER, D. N. LUTZ and H. L. BORST, who successively have been associated with him in this work.

[2] ROTHGEB, B. E. Broom Corn Experiments at Woodward, Okla. *U. S. D. A. Bul.*, 836. 1920.



RESULTS OF FIVE YEARS OF SELECTION

FIGURE 10. On the left is shown the yearly variation in percentage of central stem in four selections of broom corn, compared for the last three years with two commercial varieties, Longbrush Evergreen (L. E.) and California Longbrush (C. L.) On the right is shown the variation in length of stem in the same varieties. Yearly variation in seasonal conditions generally affects all varieties similarly, but in 1922 the amount of central stem increased considerably in the commercial varieties, and decreased in the selections. The reasons for this are discussed on page 215.

The degree of uniformity within a head-row, on the whole was decidedly greater than usually occurs in ear-rows of maize, except after inbreeding, indicating that a considerable amount of self pollination occurs naturally in broom corn as no bagging of heads was done the first year. Beginning with 1919, some heads have been bagged each year and a full setting of seed has always resulted, showing the existence of complete self-fertility. In most cases selfed seed from bagged heads has been planted, but some open pollinated heads were used when a satisfactory number of good quality bagged heads were not available.

Since 1918 selection has been continued within a few of the better strains, first for freedom from central stem and after that for good length and fineness of fiber. In 1920, and each year since then, Longbush Evergreen and another variety, California Longbrush, both secured from a commercial seedsman, have been grown in comparison with the selections. The two varieties have been propagated by compositing seed from a random sample of the marketable brush, rejecting the badly twisted and worthless stemmy heads, but including the better grade of stemmy ones.

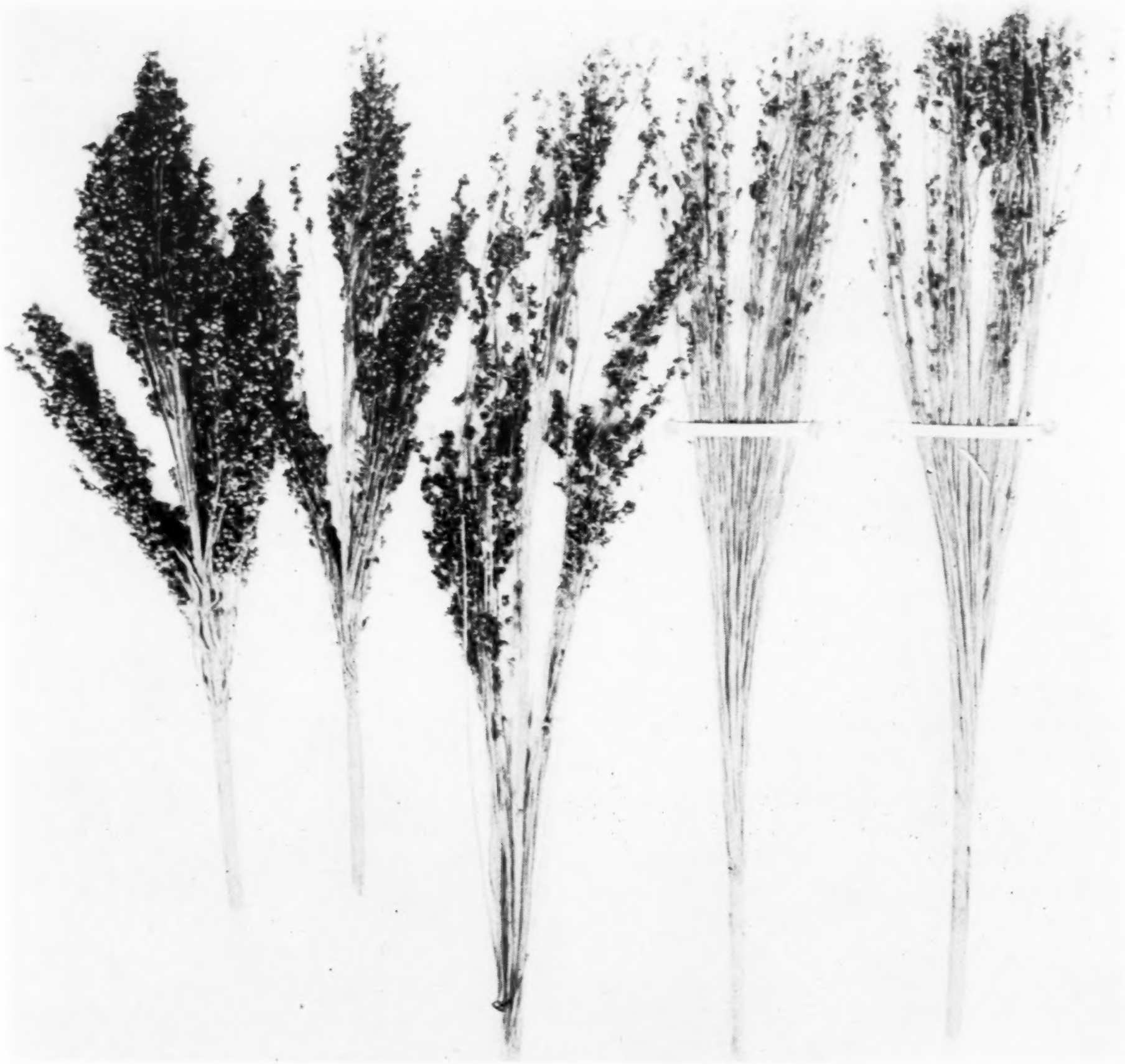
Of the original 105 heads planted in 1918 the number represented by progeny has rapidly decreased in successive years, due to the dropping out of inferior strains, until in 1921 only three remained of the good quality strains. The performance of four strains through five generations is shown graphically in Figure 10.

The values in the graphs are yearly averages of several head rows representing four of the original strains, each average involving from 100 to 1,000 plants.

Environmental Influence

That seasonal conditions have a pronounced effect on the amount of central stem and upon length of brush is evident from a study of the graphs. The values fluctuate widely from one year to another but the relative positions of the strains are fairly well maintained and all the strains and varieties show about the same kind and degree of response to seasonal influences.

The year 1920 was a very favorable crop season at Columbus, yields of small grains and of corn being high.



"CENTRAL STEM" IN BROOM CORN

FIGURE 11. On the left are shown three heads having the undesirable character, central stem. On the right are two stemless heads. Central stem greatly reduces the value of the crop because "Stemmy" heads are of small value in making brooms. The fact that seasonal conditions cause the amount of central stem to vary from year to year has led growers to believe that the kind of seed used made no difference. The present investigation shows that this is by no means true. It is quite possible to select strains that produce only a relatively small number of "stemmy" heads even in unfavorable years. As yet no strain has been isolated that is entirely free from this undesirable character.

The season of 1921 was a poor one for all grain crops, because of drought. The following year was slightly more favorable. Apparently conditions which favor long brush also produce a low percentage of stem and vice versa, though it is not easy to see just what elements in the environment produce the effect.

An exception to the uniformity of the seasonal rise and fall of the curves in Figure 10 occurs in 1922 when all the selections show a low per cent of stem, but the two commercial varieties show unusually high percentages. Also the correlation of low percentage of stem with long brush which prevails elsewhere is reversed in this case. This nonconformity of the 1922 crop is difficult to interpret. Does the small amount of stem indicate progress in the selection towards its elimination, uni-

formly effective in all three strains, or is the low stem content due to the season? Evidence that the summer of 1922 favored low stem content was obtained accidentally, and is presented herewith.

In 1922, because of severe damage to the selected seed-heads by birds and insects, it was deemed wise to plant some seed from the 1920 crop to insure continuation of the strains. This seed came from remnants saved from the previous year's planting and from some second-choice heads that had been saved over, all of which were free from central stem. The data secured from this planting show that the two-year-old seed of the three selected strains when planted in 1922 produced a crop containing 11.1 per cent of central stem, whereas essentially the same seed planted the previous year had produced 22.4 per cent of stem. This shows that the season of 1922 favored low stem content. On the other hand, the sharp rise of stem percentage in the two commercial varieties in 1922 indicates a "stemmy season." No attempt is made to reconcile the two sets of facts, unless the method of securing seed of the two commercial varieties for planting the 1922 crop was unwittingly a selection for stem.

At any rate there can be no doubt that the changed environment in different seasons has an important influence on both percentage of stem and length of brush, and it is not surprising that many growers should conclude that quality is entirely controlled by the season. Yet one only needs to study the graphs, or better still to see the quality of the crops produced year after year by some of the selections in comparison with the commercial varieties, to be convinced that heredity also is an important factor in determining the character of the crop (see Figure 12).

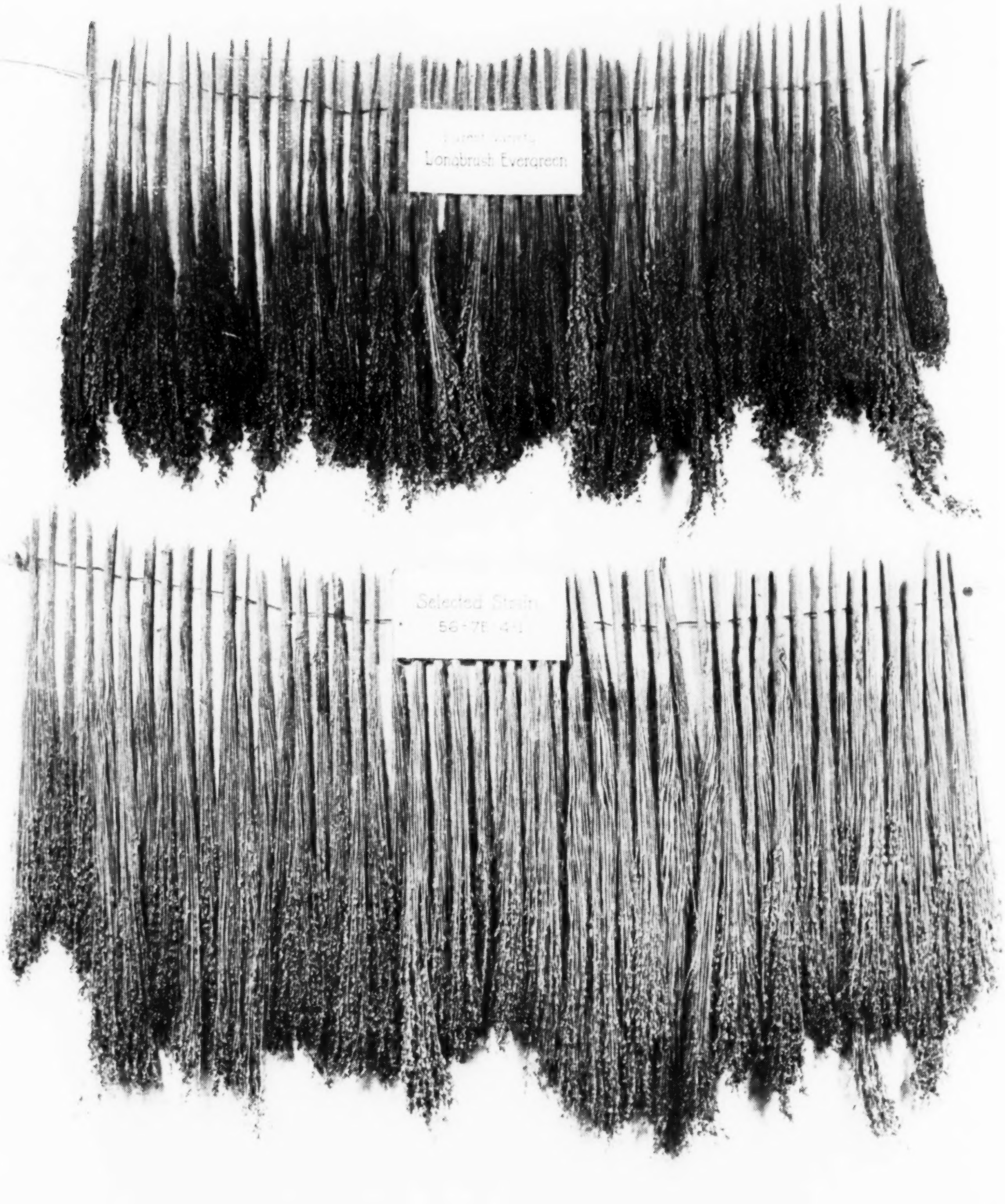
Genetic Factors

From the graphs it is evident that the three strains, 15, 26 and 56, isolated in 1917 and subjected to continuous selection for low percentage of stem, have maintained their individuality through five generations. No convincing evidence appears that these strains, after five years of intensive selection for low stem, have been changed genetically in any respect. During this time not a single head of these strains containing a central stem has been used for seed. And yet, so far as we can see through the fog of seasonal influence, they seem to have kept, practically unchanged, their original tendencies to produce similar relative amounts of central stem and lengths of fiber.

The only opportunity for making a direct comparison between two generations with environmental influence largely eliminated was the accidental one discussed above, when seed from the crop of 1920 was planted in 1922 to eke out the seed raised in 1921. The crop produced by seed of the older generation contained 11.1 per cent of stem and that of the younger contained 7.1 per cent. The significance of this difference is doubtful, although it may indicate some slight effect of selection.

The behavior of the strains as a whole strongly suggests that they are nearly pure lines. It is true there have been apparently good opportunities for selection to operate, as the different head-rows representing each strain have varied rather widely at times and only the strains which showed a low stem content were continued. Would these strains have remained at a relatively low level of stem production if continued selection had not been practiced? Our most direct answer comes from the behavior of the two commercial varieties which represent conditions of nonselection. They apparently have remained fairly constant genetically, although they are evidently made up of an admixture of strains.

In 1918 strain 4 had a relatively high stem content, but as it was desirable in other respects, stemless heads were selected for planting. In 1919 two head-rows produced respectively forty-



PROGRESS IN THE IMPROVEMENT OF BROOM CORN

FIGURE 12. This shows what has been accomplished in five years of selection. Characteristic heads of the parent strain, and of strain 56, selected from it, are shown. In 1922 the former had over six times as many heads containing central stem as the latter. The fibre of the selection is also finer, more uniform, and longer than that of Longbrush Evergreen grown under similar conditions.

nine and fifty-one per cent of central stem, which was taken to be sufficient evidence that this was a high percentage stem producer. It was then decided to try selection in the opposite direction by choosing seed heads which contained large central stems. The season of 1920 was a "stemmy season," as observed above, and these stemmy heads produced a crop that had ninety-six per cent of stem. The next year's crop contained fifty-nine per cent. A similar selection for stem had been started a year earlier in strain 45 and it produced fifty-seven and eighty-three per cent of stem in the years 1919 and 1920 respectively. All progeny of original plant No. 4 have shown a tendency toward high per cent of stem. Strain 45, however, produced some substrains that were fairly low in stem and others that were high, indicating that it was heterozygous for stem content, while strain 4 seemed to be relatively homozygous.

It seems, therefore, that the open pollinated heads selected in 1917 were largely homozygous. Subsequent head-row cultures made possible the sorting out of those which were most nearly homozygous for low stem content, and at the same time of desirable quality in other respects.

The conception of the broom corn crop gained from this experiment is that for breeding purposes it should be classed between the self-fertilized crops and the open-pollinated ones. Practical breeding, then, would begin as usual with a study of available types and varieties. From the best varieties a considerable number of desirable heads would be selected and given a progeny test in head-rows. After one or two years in head-row tests the better strains could be composited and increased; or a single strain might be increased for commercial planting. Bagging of heads is easily done and is probably worth while to insure self-pollination. There is no apparent reduction in vigor due to selfing, which is to be expected since it is shown that a large amount of natural selfing occurs. Mass selection without a progeny test in head-rows would accomplish little, or at best would make but slow progress in broom corn, for it has been shown that many good quality heads produce a mediocre or low-grade progeny. The head-row test detects these and makes it possible to distinguish between strains whose parents looked alike but were genetically different, as proved by their offspring.

It seems to be clear that central stem in broom corn is an inherited character, for different strains produce it in differing amounts; yet none has been found that produces a progeny free from this undesirable feature. Possibly multiple factors are concerned; in which case crossing of strains with low percentage of stems, followed by observation of numerous head-rows, should discover the desired stemless individuals.

That production of central stem is closely tied up with the physiological condition of the plant is indicated by our observations. When for any reason the head fails to emerge from the leaf sheath, or is retarded in its development by accident, a branch usually starts from one or more nodes of the stalk. These branches usually attain a length of several feet and produce a small, worthless brush that invariably has a central stem. Stem is always present in these branch heads, even on plants of which the partially developed main head was free from central stem. It may be that the forces which cause or allow stem to be produced in the heads of these branches are the same as those involved in the seasonal effects noted above. But further experiment would be required to make this point clear.

The method mentioned above of eliminating seasonal influence by growing two or more generations in the same season appeals to the writer as

being an important aid in many plant breeding experiments where seasonal influences obscure the effect of genetic factors. Of course, the idea is old, and has been used many times, but the method deserves wider recognition and more general use. It is best adapted to experiments with those plants that produce an abundance of seed which is viable over a period of years. With several generations of a selection experiment all growing side by side, progress could be measured with much greater accuracy than by comparing generations of plants which were grown in different seasons.

TABLE I. *The average values for certain characters in typical head-row populations of broom corn*, 1918.

Strain	Average length. Cm.	Percentage of central stem	No. of plants
30	48.7	13.0	69
50	53.6	22.7	101
15	52.9	5.9	84
102	49.8	16.0	74
56	60.4	20.2	89
2	52.0	17.3	69
4	52.6	29.4	73
45	46.3	15.7	70
84	53.1	20.9	62
16	56.2	21.3	75
46	42.8	36.6	60
7	50.9	18.8	69
3	49.3	25.2	91
103	49.5	17.7	62
86	49.5	39.7	83

The Protection of the Germ Plasm

KEIMESFUERSORGE: Entstehung und Verhuetung der Schwangerschafts-stoerungen, by DR. ALFRED GREIL, Insbruck. Pp. 27. Price, 16 cents. Leipsig, Verlag von Curt Kabitzsch, 1923.

That the child's future is largely influenced by the conditions surrounding the embyro, and particularly by the presence of various bodily poisons in the mother's blood, is Dr. Greil's thesis. This proposition is expounded in a detailed and sometimes startling way; but the treatment is dogmatic (perhaps necessarily so because of the brevity of the paper), and the reader is given no idea of the evidence behind many interesting statements. Dr. Greil holds that the gametes deteriorate rapidly after separation from their place of origin, hence the importance that zygosis should occur promptly. Thereafter, the most important feature of his program seems to be a not too nitrogenous diet for the mother. A statement of the necessary conditions for the maintenance of health in the germ-plasm is given. It is announced that an English edition of this pamphlet is in preparation; it is much to be desired that the author present some of the evidence underlying his views, since it is not generally familiar to geneticists, who will have to be shown the facts before admitting that the author's ideas are anything more than "important if true."—P.P.

A WHITE-HAIRED, BLACK-EYED MUTANT OF THE OLD ENGLISH RAT

FIGURE 13. Wild white rats were discovered at Bristol, England, in 1920. They proved not to be escaped fancy rats (*Mus norvegicus*), but were evidently a mutation of the English Black Rat (*M. rattus rattus*). Attempted crosses with *norvegicus* have not succeeded, but these white rats cross readily with the black. Interbreeding the white individuals has produced only white rats, and crosses with black rats indicate that the character is recessive to normal coat color. Females are relatively rare in this strain. The numbers available are small, but they indicate quite a wide deviation from the normal sex-ratio.

A MUTANT OF THE OLD ENGLISH RAT

F. A. E. Crew

Animal Breeding Research Department, University of Edinburgh, Scotland

WILD white rats were reported in certain warehouses in Bristol in 1920, and a well-known fancier, Mr. H. C. Brooke, of Taunton, took steps to secure live specimens. He expected to obtain feral fancy fats (*Mus norvegicus*), but to his great astonishment the rats he received were all black-eyed, creamy-white specimens of *Mus rattus rattus*, the Old English Black Rat. He ultimately obtained two Black-eyed Whites, and two Black-eyed Fawns, one of the latter being sexually immature: all four were males. A pregnant black-eyed pale-fawn female was caught, and still another black-eyed white was reported to be in the hands of a fancier of Bristol. Accurate information as to the number of the rats seen before Mr. Brooke heard of them is not available, and it is not known whether such rats are still to be found in the locality.

Below are given the results of the breeding work carried out by Mr. Brooke. Since the discovery and first description of this new variety of *Mus rattus rattus* were made by him, I propose to give the name *Mus rattus rattus* var. *brookei* to it.

TABLE I—*Crosses of the White Mutant Rats Made by Mr. Brooke.*

Parents		Offspring					
		Black		*brookei*		agouti	
♂	♀	♂	♀	♂	♀	♂	♀
1. *brookei* (w) × wild black		4	3	—	—	—	—
2. *brookei* (w) × wild white-bellied agouti		—	—	—	—	5	4*
3-6. *brookei* (w) × F1 from (2)		1	—	7 (w)	3 (w)	6	4
7. *brookei* (f) × wild yellow-bellied agouti		—	—	—	—	3	2+
8. *brookei* (f) × F1 from (7)		—	1	2 (f)	3 (f)	1	—
9. *brookei* (w) × wild black (extracted)		—	1	—	—	3	1
10. *brookei* (w) × heterozygous black		3	3	6 (w)	2 (w)	—	—

w, white; f, fawn. *Mr. Brooke reported that some of these were white- and others grey-bellied; + that some were grey- and others yellow-bellied.

TABLE II—*Results of Breeding Work With White Mutant Rats in the Animal Breeding Research Department*

Parents		Offspring			
		Black		*brookei* (white)	
♂	♀	♂	♀	♂	♀
1- 4. *brookei* (w) × wild black		13	18	—	—
5- 6. F1 from (1-4) × F1		4	6	2	—
7-12. *brookei* (w) × F1 from (1-4)		10	8	12	3

Many *brookei* × *brookei* matings were made and invariably yielded nothing but creamy-white black-eyed individuals, but it was remarkable that females were relatively rare.

Mr. Brooke sent some of the males to me and the results of the breeding work carried out in this Department are given below.

The rarity of the *brookei* female is again noteworthy.

Several matings of *brookei* × *brookei* have been made and the progeny are invariably black-eyed creamy-whites, no matter how the parents were obtained.

The outstanding characteristics of this new variety of *Mus rattus* are the bulging jet-black eye, the creamy-white body color, and the slaty color of the skin of the ears and tail. Every opportunity has been offered both by Mr. Brooke and by myself for the mating of these rats with the fancy rat (*norvegicus*), but no such mating has occurred. The two species live together harmoniously and will foster each other's young. Individuals fostered by tame *norvegicus* does and handled frequently from their earliest days become just as tame as their foster parents and give up their nocturnal habits.

The breeding results suggest that the mutant variety of the Old English Black Rat has a coat color which behaves as a recessive character when tested against the black coat color of the parent stock.

The specimens referred to as fawns were not quite similar in color to fawn "fancy" rats or mice, being more biscuit-colored. They were also rather paler than the Fawn *Rattus rattus* produced by Hagedoorn and Bonhote, differing from the latter also in that their eyes were always black, whereas Bonhote records of his Fawns that their eyes were dark ruby when young, darkening with age as in the Cinnamon Canary.

A British Journal of Experimental Biology

HITHERTO there has existed in Great Britain no journal which served specifically for the publication of researches in experimental biology lying outside the confines of genetics on the one hand, and traditional human physiology on the other. American workers who have created a powerful impetus towards experimental inquiry in biological science will, it is hoped, welcome the announcement that a British Journal of Experimental Biology will appear in September, 1923, issued by Messrs. Oliver & Boyd, from the Animal Breeding Research Department at Edinburgh. While a primary object of the Journal will be to promote in Great Britain the extension of inquiry along experimental lines, it is the earnest hope of the Editorial Board that American and continental scientists will give their support not only by subscribing but also by offering contributions for publication.

All communications should be addressed to the Managing Editor, the Animal Breeding Research Department, the University, Edinburgh, Scotland.

F. A. E. Crew,
W. J. Dakin,
J. Heslop Harrison,
Lancelot T. Hogben,
Julian S. Huxley,
J. Johnston,
F. H. A. Marshall,
Guy C. Robson,
A. M. Carr Saunders,
J. MacLean Thompson.

IN THE MELTING POT

IT HAS long been charged and to a large extent proved that the immigration of recent decades into the United States, coming of late years largely from the Mediterranean region and the Near East, is eugenically below the average of the older immigration, and of the American stock of native parentage, both of them largely Nordic in composition. Army mental tests proved this clearly as to general intelligence,[1] but the fact can be tested in many other ways.

The House of Representatives Committee on Immigration and Naturalization has been holding hearings during the past winter, and called on Harry H. Laughlin, superintendent of the Eugenics Record Office, for information as to the foreign-born in institutions for the defective and delinquent in the United States. His testimony has been issued by this committee, and forms a pamphlet[2] of 106 pages packed full of interesting information.

Dr. Laughlin's method of attack was to calculate a normal quota for each group of foreign-born in the United States, in a classification which embraced all the principal countries of the world and ran up as high as No. 67, "born at sea."

Taking a given institution population,—say the feebleminded,—the percentage of this population to the total population of the United States was taken as 100. Then if the Italians, for instance, represented (as measured by the 1910 census) 1.46 per cent of the total population of the United States, it was calculated that they ought to represent 1.46 per cent of the total population of the feebleminded institutions in the country, if their showing in this respect were "normal." The extent to which any group exceeded or fell short of its quota, calculated in this way, was taken as indicating its standing in comparison with the United States population as a whole, and with other groups figured in the same manner.

The statistical difficulties of interpretation of such figures are quite obvious, and doubtless no final validity would be claimed for any of them. To follow up the illustration already adopted, it is clear that the extent to which the Italians fell short of or surpassed their quota would be influenced by such important factors as the age and sex of immigrants, the regions in which they settled in the United States, the tendency of race or religion to take care of its own dependents, and the like. While such questions make all comparison provisional, Dr. Laughlin is undoubtedly justified in claiming that where a group's "quota fulfilment" exceeds 200 per cent, in connection with a small probable error (which he calculated in all cases), that group deserves further examination from the point of view indicated.

The Italians—to conclude with the illustration chosen, were entitled to 247 inmates of feebleminded institutions, but only 64 were found. In this respect, then, they fulfilled their quota to the extent of only 25.4 per cent. As compared with the population at large, it appears that the Italian immigrants either have a small per cent of feebleminded, or else their feebleminded for some reason do not get into America's public custodial institu-

[1] See Popenoe, Paul. Intelligence and Race: A review of some of the results of the army intelligence tests. I, the foreign born. *Journal of Heredity*, Vol. XIII, No. 6, pp. 265-9, Washington, D. C., June, 1922.

[2] "Analysis of America's Modern Melting Pot." Hearings before the committee on immigration and naturalization. House of Representatives, 67th Congerss, 3rd session, November 21, 1922, Serial 7-C. Statement of Harry H. Laughlin, Washington, Government Printing Office, 1923.

tions; or both explanations may conceivably apply.

The fact is that nearly all of the foreign-born groups fell short of their quota for feeblemindedness—a fact without much significance when it is remembered that only a fraction of one per cent of the estimated number of feebleminded in America is to be found in custodial institutions. The Serbians make the worst showing, with a quota fulfillment of 220.62 per cent.

Segregation of the insane is fairly complete, hence the data under this head should be more significant. All foreign groups except Japan, China, and Switzerland exceed their quotas, running up to such high percentages as

Turkey	200.12
Russia, Finland and Poland	265.1
Bulgaria	300.19
Ireland	305.2
Serbia	400.34
Mexico	549.6
Spain	660.21
Serbia	1400.2

The reasons for the excessive prevalence of foreign-born in American hospitals for the insane have been abundantly discussed, and it is not necessary to enter into them here. Unquestionably part of the explanation is that peasants from a simple environment find the stress of American life, especially in the cities, too much for them.

The statistics of crime are even more instructive. All the Nordic countries stand well, falling notably short of their quotas; and the foreign-born as a whole do not quite reach their quota (98 per cent fulfillment). The bad showing of certain countries is therefore all the more conspicuous. In addition to the American negro (207 per cent), the groups which more than double their quotas are:

Italy	218.2
Turkey	240.17
All Asia	251.7
All Balkans	275.6
Greece	293.9
West Indies	318.14
China	337.12
Bulgaria	366.26

This showing is based on records of the inmates in 155 state and federal institutions. In some cases it may be that a given race is discriminated against in law enforcement in some parts of the country, but this can not explain away all of the cases. On the whole, it can hardly be doubted that certain of the countries from which the United States has drawn a large immigration during the last quarter century have been sending their dregs.

The small figures published for epilepsy indicate that the bulk of the institutional inmates are native born. As to tuberculosis, the Balkan states (379 per cent) and Greece (436 per cent) are naturally topped by the American Indians (573 per cent). In blindness, deafness, and deformity the foreign-born are less represented than the native-born. As a rule, persons with such deformities would not come as immigrants, and would not be admitted if they came.

For self-preservation, it would seem that the United States has the right, and the duty, to require that immigrants shall be superior to the average, rather than inferior. Evidence from many different sides indicates that during the decade or two prior to the recent restriction laws, the immigration tended to be more inferior. The present restrictive (three per cent) law tends more or less indirectly to bring in a better quality of immigrants, but it is generally admitted that other measures of selection as well as restriction are desirable. The ideas of one student of this question are given in the testimony of Dr. Laughlin on this point:

> In addition to the medical requirements now listed, there should be added an examination into the potential parenthood of the immigrant for the purpose of determining whether, in the normal course of future years, in the United States, the immigrant is physically capable of becoming a parent.

2. The standards of mental ability and personality should be measured by a series of modern psychological tests.

3. The reputation of the immigrant in relation to his home community should be considered.

4. The family history of the immigrant should be made an important factor in judging of his future personal worth, and of the hereditary qualities which he would probably pass on to his children.

5. The American people should establish a system of "immigration attaches" and "immigration passports" in our consular service. Data on personal and family history and on reputation should be required by and should be furnished to the "immigration attache" who would vise the "immigration passport." only in case the immigration standards of the American nation were met in every way. The additional requirements which I have just listed would go a long way toward establishing the standards which the American people desired to see adhered to.

6. The immigrant should be registered, and a registry should be maintained of all foreign-born in the United States. The immigration admission paper should be the first registration card, which should be retained by the alien, and annually examined by the United States, until the immigrant becomes a citizen of the United States, or until he dies or is deported.

7. The deportation system, which is the object of a survey now being completed, is the last line of defense in our national battle against undesirable alien qualities. If an alien remains, legally or illegally, in the United States for five years or longer, we can not deport him; but we must keep him and his progeny indefinitely for better or worse. We should admit and welcome superior qualities of body and mind in aliens, but, at the same time, we should exclude the undesirables, and if by chance some undesirables get in, despite our efforts at exclusion, we must deport them.

It should be possible to control immigration in such a manner that every immigrant would constitute a natural asset: first, a present economic asset; second, a future social asset; third, an asset to the natural hereditary qualities of the race in case the immigrant becomes the parent of sound and intelligent offspring.

PAUL POPENOE.

Books Received

Proceedings of the Second International Congress of Eugenics, Volume 1, *Eugenics, Genetics and the Family;* Volume 2, *Eugenics in Race and State.* Williams and Wilkins, Baltimore, 1923.

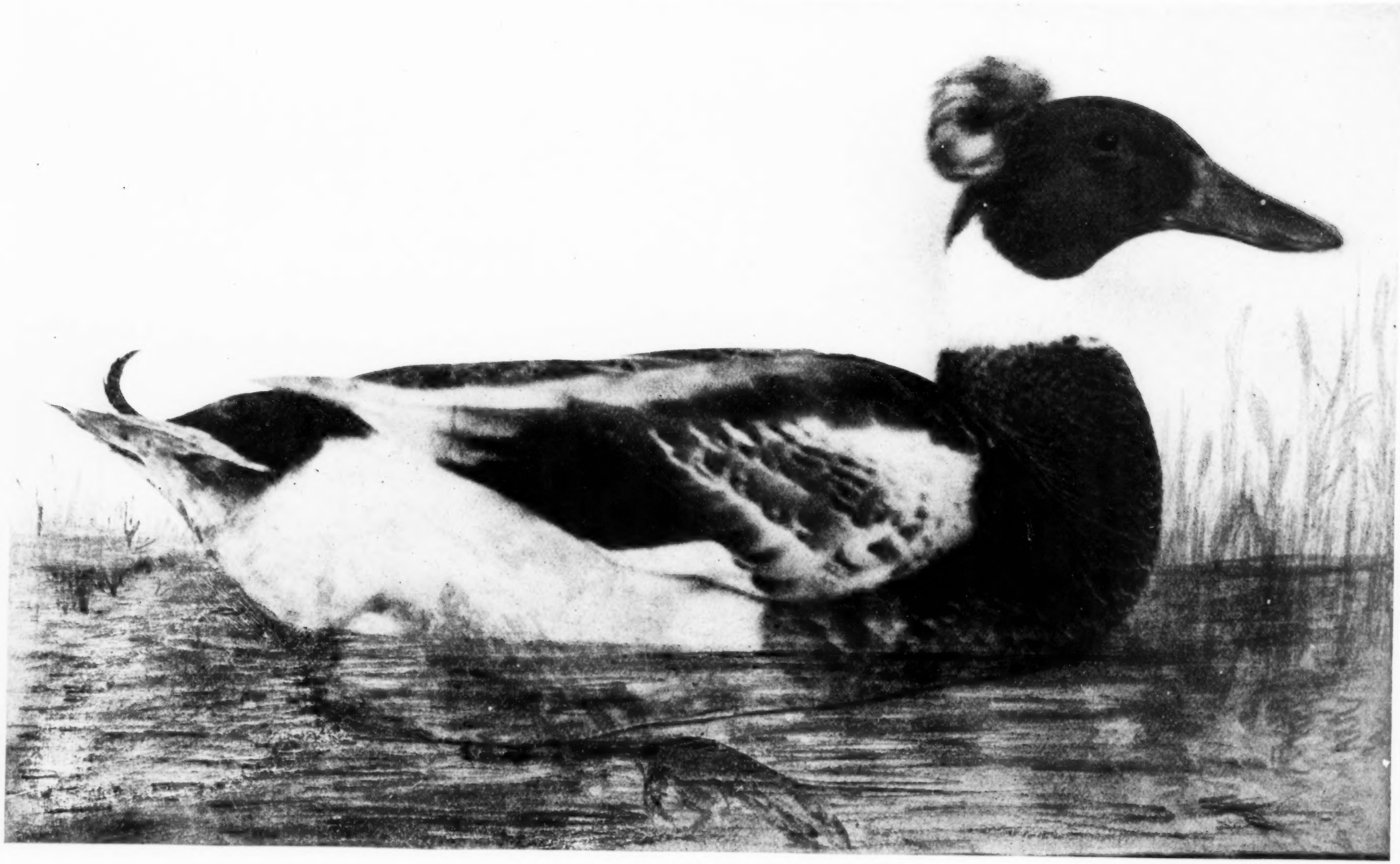
Studies in Mental Deviations, by S. D. PORTEUS. Publication Number 24 of the Training School, Vineland, N. J.

Heredity in Poultry, by REGINALD CRUNDALL PUNNETT. The Macmillan Company, New York and London. 1923.

Of What Use Are Common People?, by HEINRICH BUCHHOLZ. Warwick and York, Baltimore. 1923.

The Index to Volume XIII

The index to Volume XIII is not yet ready, but is now in preparation and will be mailed to members shortly. The regrettable delay in its publication has been occasioned by the unexpected closing of the last volume, a greatly increased amount of work having been entailed by the changes made at that time.



A CRESTED MALLARD DRAKE

FIGURE 14. On the head of this drake is a soft topknot of feathers, quite unlike the crests found in certain wild species of ducks. Darwin noted the existence of such tufts, and stated that the skulls of the tufted individuals were rounder than usual, and that they were perforated with numerous small holes. No data are available as to how this character originated, or is inherited, and any information on these points would be appreciated by the author.

CRESTED DOMESTIC DUCKS

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VARIOUS species of ducks in nature are crested, their crests being, as a rule, composed of elongate, soft, feathers, directed backwards, and only partially raised during certain moods of the bird. Mandarin ducks of the Orient possess such a crest, as does, to some extent, our own wood duck. However, no wild duck known to me has such a crest as the one shown in the illustration. I brought this bird home alive from Center Market, Washington, D. C., early in November, 1922, it being a drake mallard of great size, doubtless due to the fact that it came from a stock into which had been bred other species noted for that character.

At the middle point at the back of the head of this mallard was a soft, roundish ball of feathers, which has generally been referred to as a "crest;" though, as a matter of fact, it is no such crest as we meet with among wild ducks or their near allies, such as the hooded merganser and those anserine species that possess soft and drooping crests. Many ducks are exposed for sale in the Center Market at all times of the year, and I pass, almost daily, the place where a great many of them may be seen in crates; but I may say that in the course of a year or so I have not observed more than three or four having such a crest as is here shown in the figure. I borrowed the bird from the dealer, made the photograph of which the accompanying figure is a reproduction, and returned the loan.

Now comes the question as to how such a crest could have originated in a line of ducks, either ferine or domesticated, when they are noted for being especially devoid of such a feature. No mallard in nature ever exhibited such a crest—nor does any other species, in so far as I am aware. Breeders of domestic ducks appear to be entirely ignorant of its origin; they say it is a "freak," which means nothing. The statement fails to explain anything; and, freak or no freak, it must have arisen somehow.

In referring to this particular character, Darwin made the statement that in some ducks "a tuft of feathers on the head is by no means a rare occurrence; namely, in the true tufted breed, the hook-billed, the common farmyard duck, and in a duck having no other peculiarity which was sent to me from the Malayan Archipelago. The tuft is only so far interesting as it affects the skull, which is thus rendered slightly more globular, and is perforated by numerous apertures."* This statement in no way *explains* the origin, or probable origin, of such a crest; and it further complicates the question through announcing what is to be found in the skull of ducks possessing such a crest.

Up to the present time I have not examined the skull of a duck having one of these feathery topknots—in any event it is quite secondary to the matter of the presence of the crest and the manner of its origin. I note that Darwin did not take up that matter; and so far as I know, he left no explanation as to how such a crest came about.

Should any reader of THE JOURNAL of HEREDITY possesses information on this point, I would be very glad to know about it.

* Animals and Plants Under Domestication, Vol. I, p. 339.

perforated with numerous small holes. No data are available as to how this character originated, or is inherited, and any information on these points would be appreciated by the author.

THE GENETICS OF JACOB

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THE science of genetics is twenty-one years old, but the foundations upon which genetics rests are very old indeed. The very beginnings are prehistorical, and enough information on heredity was early acquired to give rise to certain systems of selection in animal breeding.

Jacob, for example, was able to mulct his father-in-law through a definite system of selection and mating. That Jacob was in advance of many in his time there is little doubt, and also there is little doubt that he did not care to have his associates learn the secret of his success. He was, throughout his whole life, mainly concerned with the advancement of Jacob and Jacob only. Although we may agree that this son of the chosen people was a consummate rogue, we often do him injustice on the score of knowledge.

In the book of Genesis 30:27-42 there is set forth in detail a system which Jacob is supposed to have used in order to influence the color of his flock. This passage is often cited to show that Jacob believed in the efficacy of maternal impressions. A careful reading of the chapter shows that he realized the importance of segregation, as he put three days journey between his spotted herd and the flocks of Laban. Furthermore, this account has been written by an observer not concerned in the material aspect. We get a clearer understanding of Jacob's notions concerning breeding if we read Genesis 31:8-14, which purports to be Jacob's own account of his procedure:

"If he (Laban) said thus. The speckled shall be thy wages; then all the cattle bare speckled; and if he said thus. The ring-straked shall be thy hire; then bare all the cattle ring-straked. Thus God hath taken away the cattle of your father and given them to me, and it came to pass at the time that the cattle conceived, that I lifted up mine eyes, and saw in a dream, and *behold* the *rams which leaped upon* the *cattle were ring-straked,* and *speckled* and *grizzled.* And the angel of God spoke to me in a dream saying, Jacob, and I answered, Here am I. And he said, lift up now thine eyes and see, all the *rams* which *leap* upon the *cattle* are *ring-straked, speckled* and *grizzled,* for I have seen all that Laban doeth unto thee."

Jacob had been "stung" in his first contract with Laban. He had labored fourteen years to make good his slip and all this time had been trying to devise a means whereby to provide for his family. As a result of long brooding while tending his herds his "inspiration" came in a dream: Mixed breeding and isolation. To how many scientific men has the solution of a difficult problem come in the same way?

Taking the two chapters together it would seem that Jacob had observed the results of cross breeding, and probably also observed what took place when both parents were of the same type. Of course, we cannot now make a genetic analysis of Laban's cattle, but if "ring-straked, speckled and grizzled" are assumed to be dominant characters, we must recognize that Jacob's breeding methods were not based altogether on superstition. He realized the value of isolation and had some knowledge of the importance of giving the get an opportunity to develop under the most favorable conditions. Since the modern breeder makes use of the same principles it indicates that the art of breeding was fairly well advanced at that early period.—1746 (?) B. C.

THE INHERITANCE OF DEGREES OF SPOTTING IN HOLSTEIN CATTLE

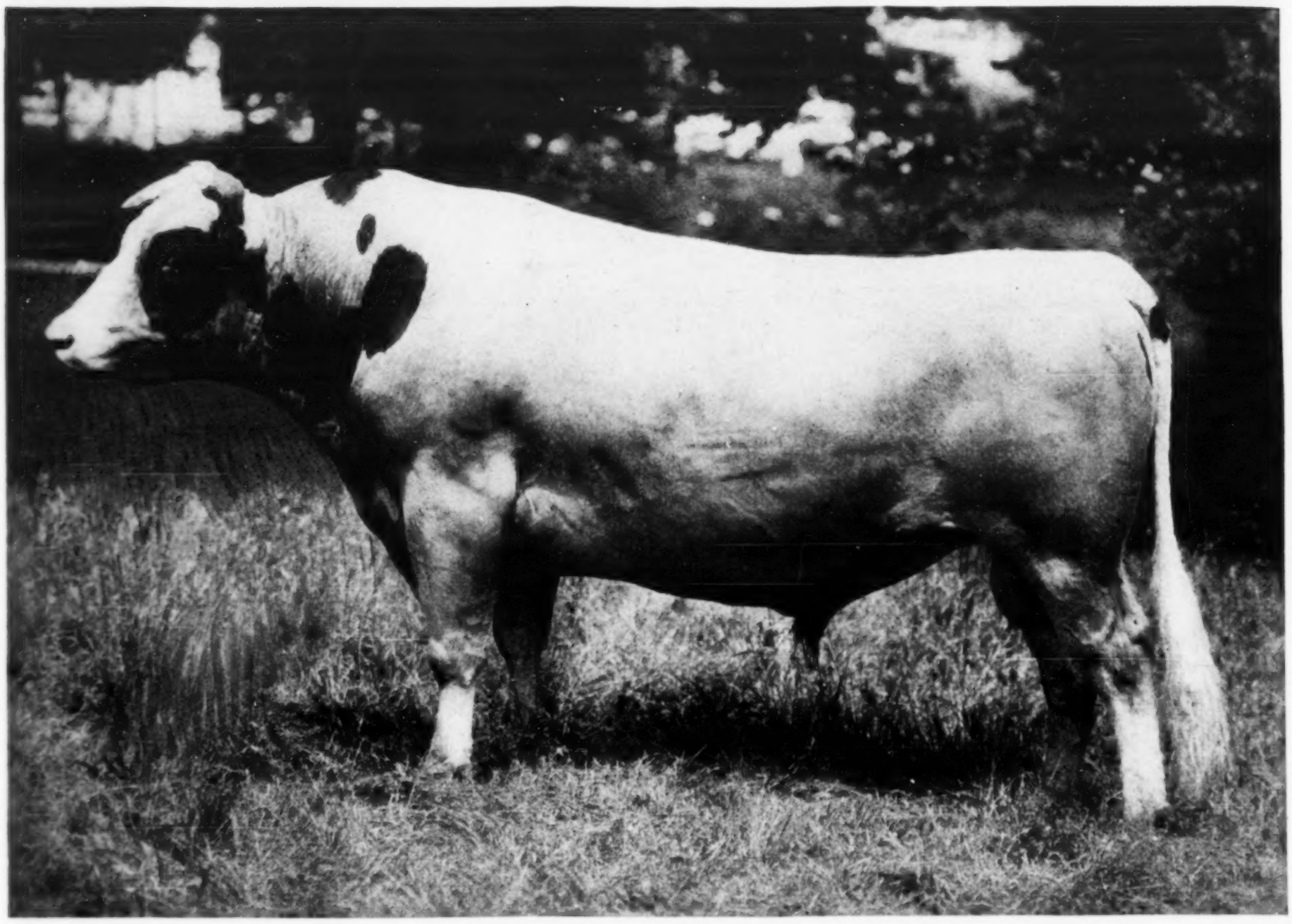
L. C. Dunn, H. F. Webb and M. Schneider
Storrs Agricultural Experiment Station[1]

HOLSTEIN cattle, with their striking black and white coloration, are familiar features of almost every country landscape. Purebred Holsteins in the United States outnumber all other kinds of purebred dairy cattle combined and supply the greater portion of the milk and dairy products consumed in this country. In addition to mere numbers, they are interesting to the student of natural history because of the great variety of coat patterns in existence. Unlike other breeds, they have never been made to conform to a rigid standard of pattern. In fact, Holstein breeders have rather prided themselves on the absence of requirements in regard to coat pattern and have preferred to direct their breeding operations toward the perfection of a valuable milk producing type, uninfluenced by minor considerations of pigmentation. The only registry requirements relating to spotting are that the animal to be registered must be black and white; and that the following extremes of spotting are barred from registration: (1) solid black, (2) solid white, (3) black switch, (4) solid black with white only under belly, (6) black on legs beginning at feet and extending to kness and hocks or black with white interspersed in these parts. The relative amounts of black and white may and do vary within wide limits from nearly all white with black eyes, to almost solid black with traces of white on the extremities or belly. There has been of late years a tendency for some Holstein breeders to prefer the lighter types, while a few have favored the very dark types. These preferences have not been general and they have not influenced the breeding operations nor changed the general character of the breed to any marked degree.

The occurrence of nearly all degrees of black and white spotting provides additional marks of identification of the individual animals. Breeders have taken advantage of this fact and have kept sketch records of the spotting of each animal, and have made wide use of photographic methods for recording the type and coloration of their cattle. The Holstein-Friesian Association, which is the official registry office for this breed, now requires a standardized sketch of each animal submitted for registry and when one considers that over one million purebred animals have been registered, each entry accompanied by a descriptive sketch and a statement identifying both parents of the animal, the bulk and value of these records may be readily recognized.

In view of this wealth of interesting material, we were somewhat surprised to find, about a year ago, that the inheritance of the variations in the coat pattern of this breed had never been investigated. We decided to attempt such an investigation and Mr. Webb, then a student in the Connecticut Agricultural College, undertook to gather the necessary data as thesis material for an advanced course in genetics. He met with prompt and courteous cooperation from the officers of the Holstein-Friesian Association who placed the material in their registry office at Brattleboro, Vermont, at his disposal. It is also a pleasure to acknowledge here the help and suggestions of Professor G. C. White and Mr. L. M. Chapman of the Dairy Department of

[1]Contributions in Genetics No. 16.



THE LIGHT SIRE

FIGURE 15. King Model 18717 is a noted producer of superior offspring. He has about fifty units of black (roughly about five per cent) on each side of the body. By cows like himself he produced only light calves. By dark cows he produced medium and dark offspring. This is evidently the recessive color pattern in Holstein cattle. The few light calves produced in crosses with dark cows were doubtless due to the heterozygous condition of the dark parent. Photograph by courtesy of the Bloomingdale Farms, Somerville, N. J.

the Connecticut Agricultural College. Several leading breeders of Holstein cattle and the editor of the Holstein-Friesian World have very kindly supplied information and photographs. Their courtesy is acknowledged in the legends to the illustrations.

The Problem

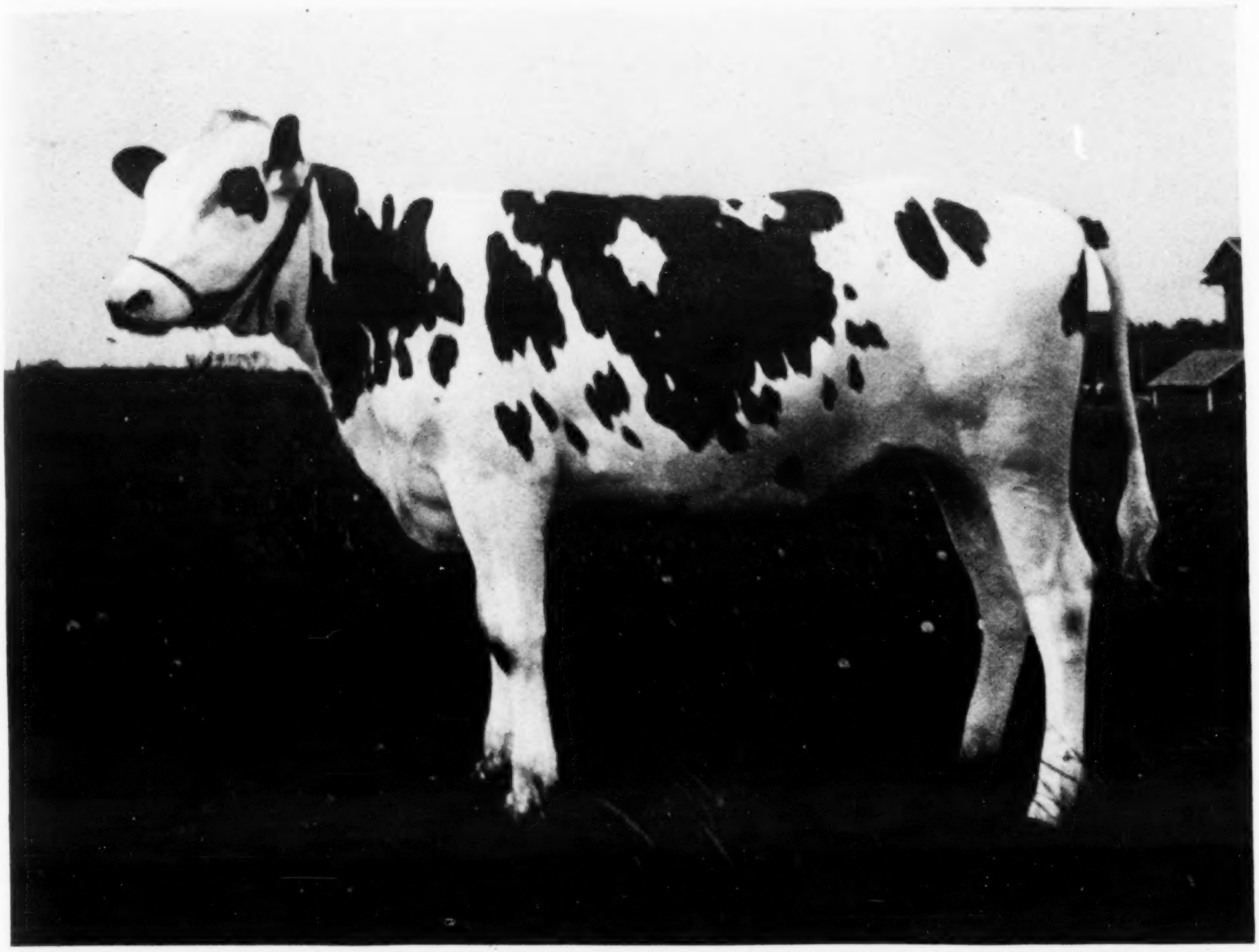
The problems which we set out to study were:

(1) To define and describe the variations in the gross amounts of white spotting in Holstein cattle. The best preliminary information could be obtained, we found, from a study merely of the relative areas of black and white spaces in the coat, disregarding for the time, the variations in the character or arrangement of the spots.

(2) To find out whether variations in the amount of spotting were inherited.

(3) If inherited, in what manner.

Our plans for attacking this problem were more or less conditioned by the form in which the data were available. We decided that the most feasible plan was to choose individual males showing great differences in the amount of spotting, and to obtain for each male (1) his spotting description, (2) the description of a random sample of cows of all degrees of spotting with which he had been mated, and (3) the description of one or more offspring from each of these matings. This should provide a number of sire-dam-offspring trios, and should afford a test of the genotypes of the males, at



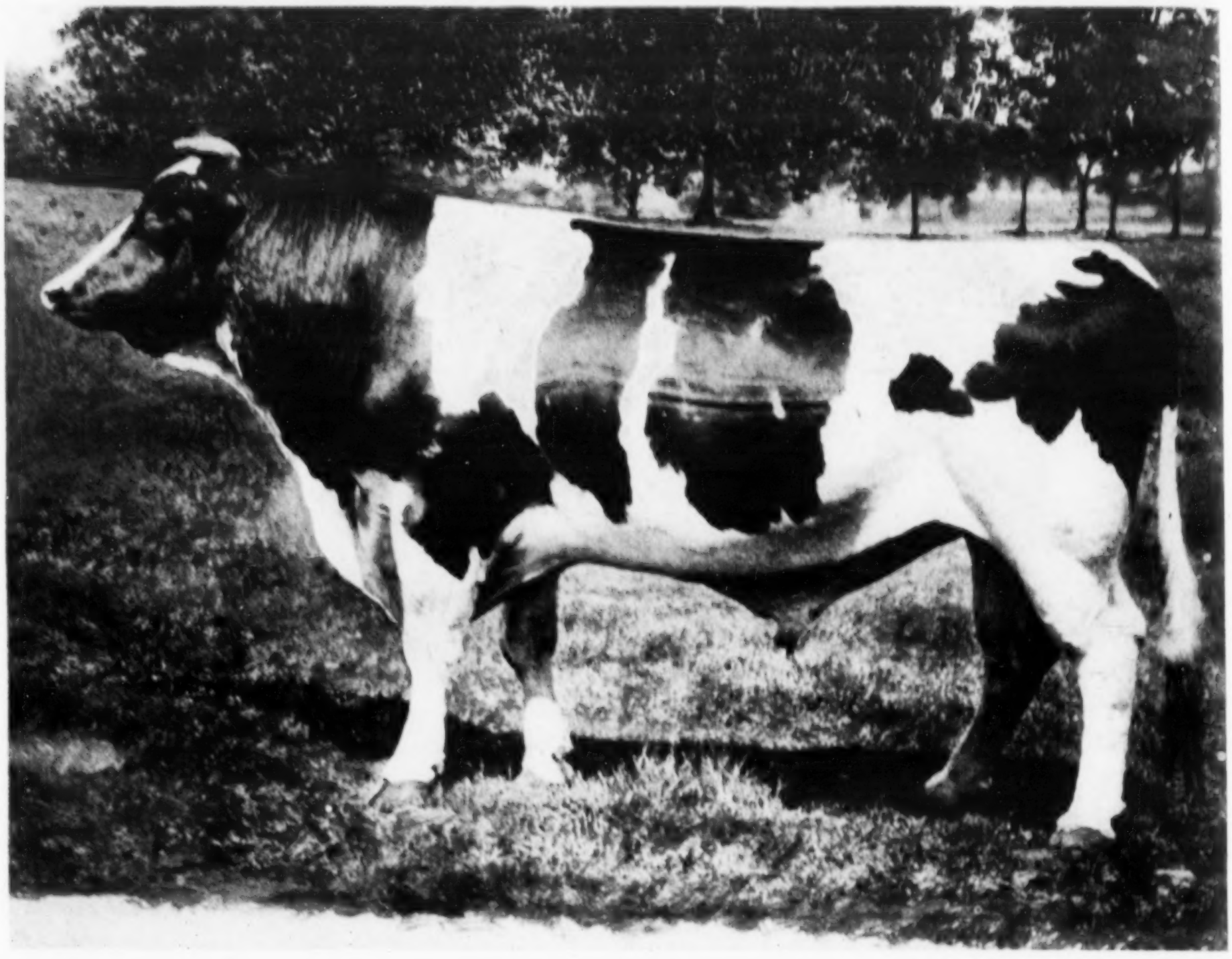
AVERAGE DEGREE OF SPOTTING OF THE LIGHT SIRE'S DAUGHTERS

FIGURE 16. This daughter of King Model (Bloomingdale Model Ormsby Segis 598203), shows the average grade of his daughters by all grades of cows. She has 201 units of black (about twenty-one per cent) on each side of the body. In all three bulls studied, the average color of offspring was intermediate between the grade of the sire and the avearge grade of the dams. Photograph courtesy of Bloomingdale Farms, Somerville, N. J.

least. Because of the small number of recorded offspring which could be obtained from any one female, it did not appear profitable with the time at our disposal to attempt to determine the genotypes of individual females, although we realized that this would eventually be a necessary step.

Methods of Obtaining Data

All of the evidence used in this study was obtained from the individual registry certificates in the office of the Holstein-Friesian Association at Brattleboro, Vermont. These certificates contain among other things the registry number of the animal, registry number of sire and dam, and a sketch of the spotting of the animal drawn on a standardized diagram. The accuracy of the parentage records of these animals need not be questioned since this is a matter of considerable concern to the registry office and is checked by them. The sketch of the animal is made by the breeder and although checked by an independent observer, is admittedly an approximation. It is sometimes rechecked when the animal is sold and a new registry certificate made out; and in such cases the agreement of the two records is reasonably good. The original sketches are nearly all made from young animals and some variation from this is to be expected when the same animal is resketched after attaining full size. The officials of the



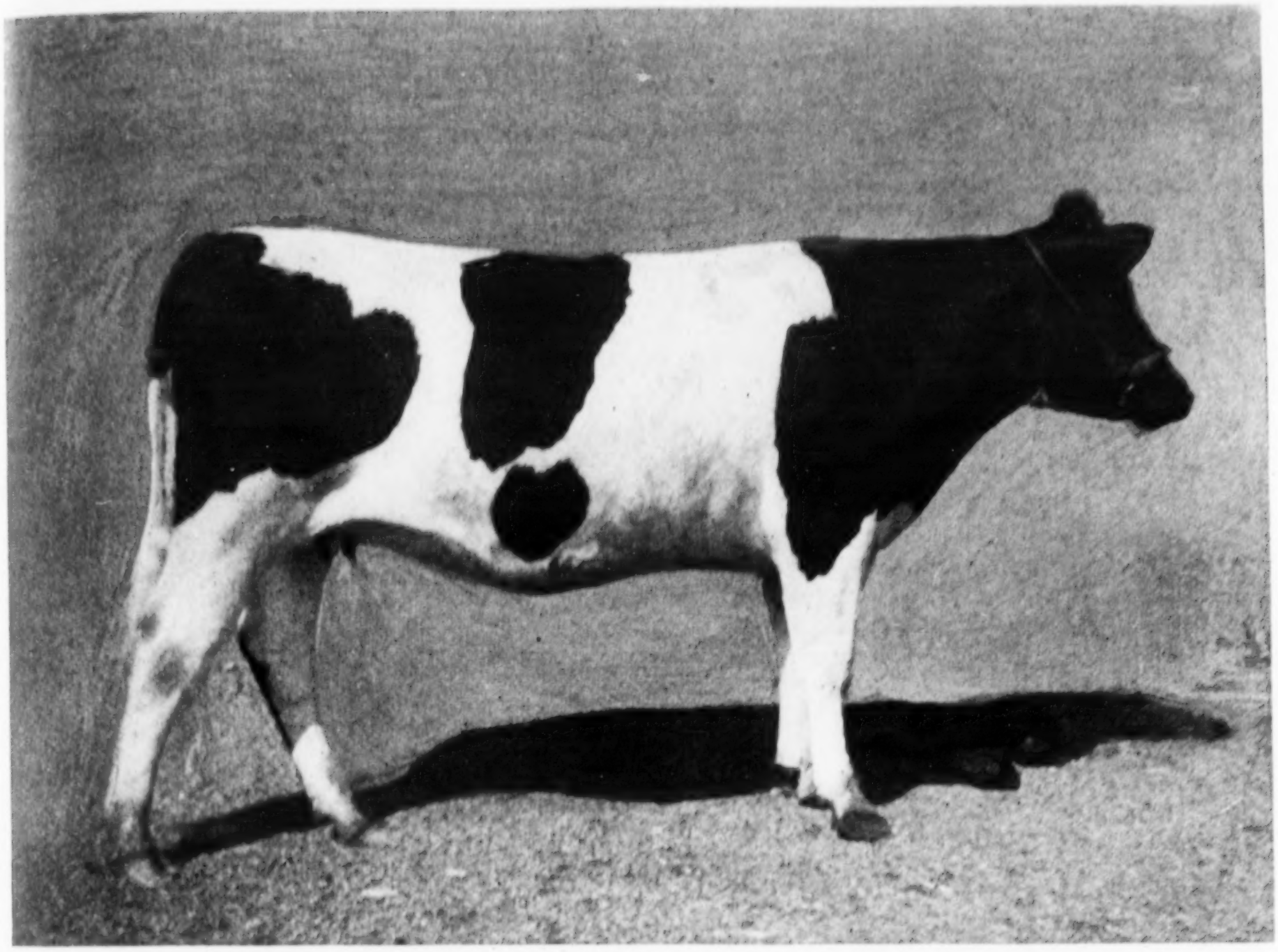
THE MEDIUM SIRE

FIGURE 17. King of the Pontiacs has about 350 units of black and although medium in appearance he bred more like a dark bull which was a hybrid, carrying latent factors for the lighter grades of spotting. This famous sire has 280 registered daughters. Bred by Stevens Hastings Co., Lacona, N. Y. Photograph courtesy of Mr. Stevens and the Holstein-Fresian World.

registry office believe the sketches to be fairly accurate on the average. The error in estimating the amounts of black and white present in the coat is probably not over five or ten per cent.

The spotting of each side of the animal is sketched separately on a standard profile diagram. Our method was to trace each sketch on onion skin paper. We then prepared a duplicate blank diagram on fine co-ordinate paper. The area occupied by the profile diagram was about 950 squares. The extent of the black and white spaces on each animal could then be estimated by applying the onion skin sketch to the ruled diagram and counting the number of squares covered by the black and white areas. This was done for both sides of all animals used in this study. The results for each estimation were then expressed as the number of units or squares of *black* on the animal. An all white animal would then be grade 0, while an all black one would be 950. The very light bull in Fig. 15 is of grade 50. The units in this case are 950ths of the total profile area of the animal, or practically per milles. Dividing each grade by ten reduces it roughly to per cents. Thus King Model (Fig. 15) is of grade 50 or roughly 5 per cent black.

The spotting grades of 294 animals are used in this study, divided as follows:



AVERAGE DARKNESS OF MEDIUM BULL'S OFFSPRING

FIGURE 18. Alcartra Johanna Korndyke 415274 shows the average grade of the daughters of King of the Pontiacs when mated to cows of all grades. The cows with which King of the Pontiacs were mated averaged 200 units (about twenty per cent) darker than the cows with which the other two bulls were bred. Photograph courtesy of the Bloomingdale Farms.

(1) A light bull (King Model) Figure 15:

46 cows mated to King Model and 50 offspring (25 males 25 females) resulting from these matings, including one pair of twins and two offspring each from three cows.

(2) A bull of medium grade (King of the Pontiacs) Figure 17:

49 cows mated to King of the Pontiacs and 49 offspring (25 males and 24 females) resulting from these matings.

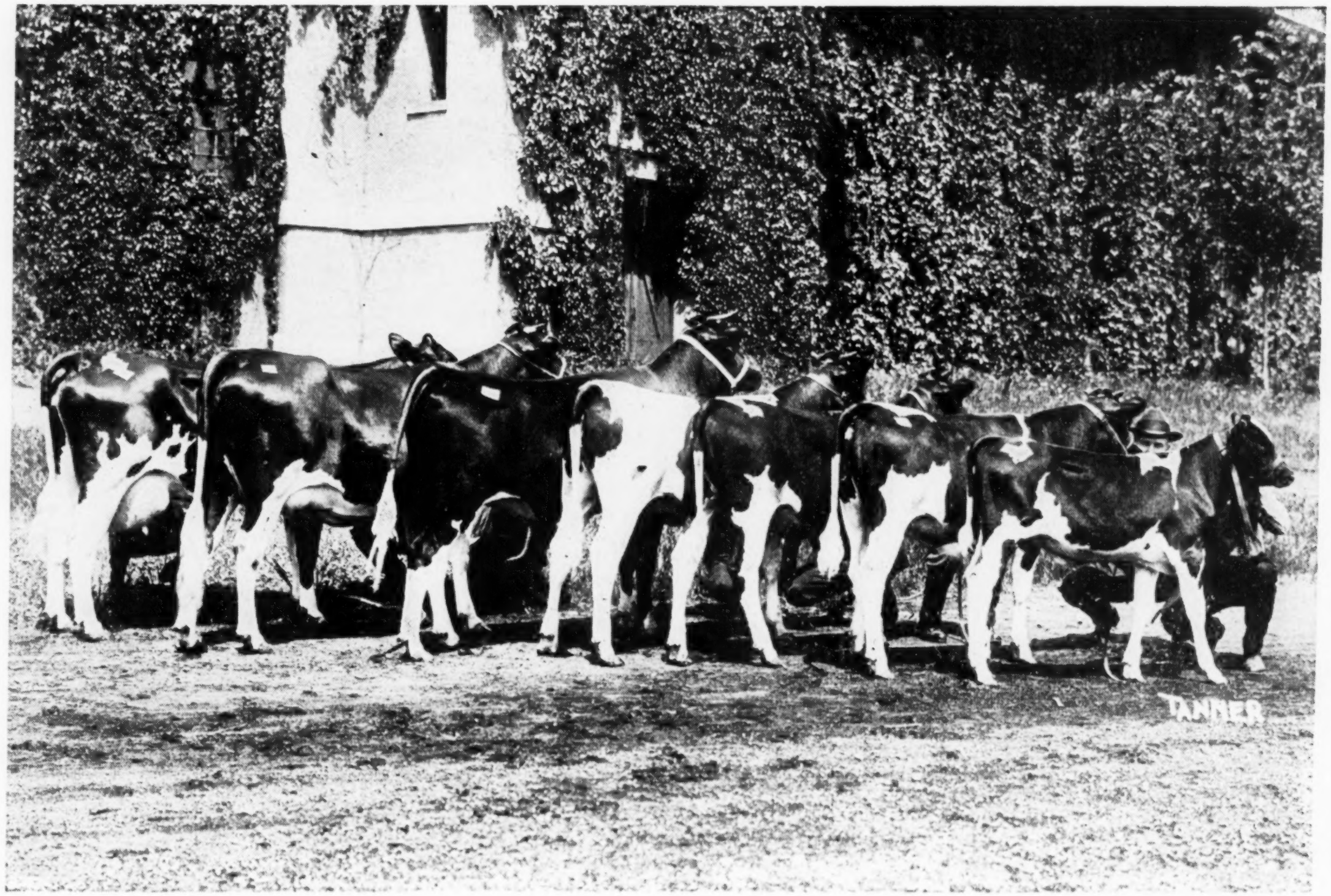
(3) A dark bull (King Pietertje Ormsby Piebe) Figure 20:

47 cows mated to King Pietertje Ormsby Piebe and 50 offspring (25 males and 25 females) from these matings, including 1 pair of twins and two offspring each from two cows.

The cows which had been mated to each bull were chosen by serial registry numbers in order that a random sample in respect to spotting might be secured. In order to secure an equal number of male and female offspring, the dams of the first twenty-five offspring were chosen as dams of female calves and the second twenty-five as dams of male calves.

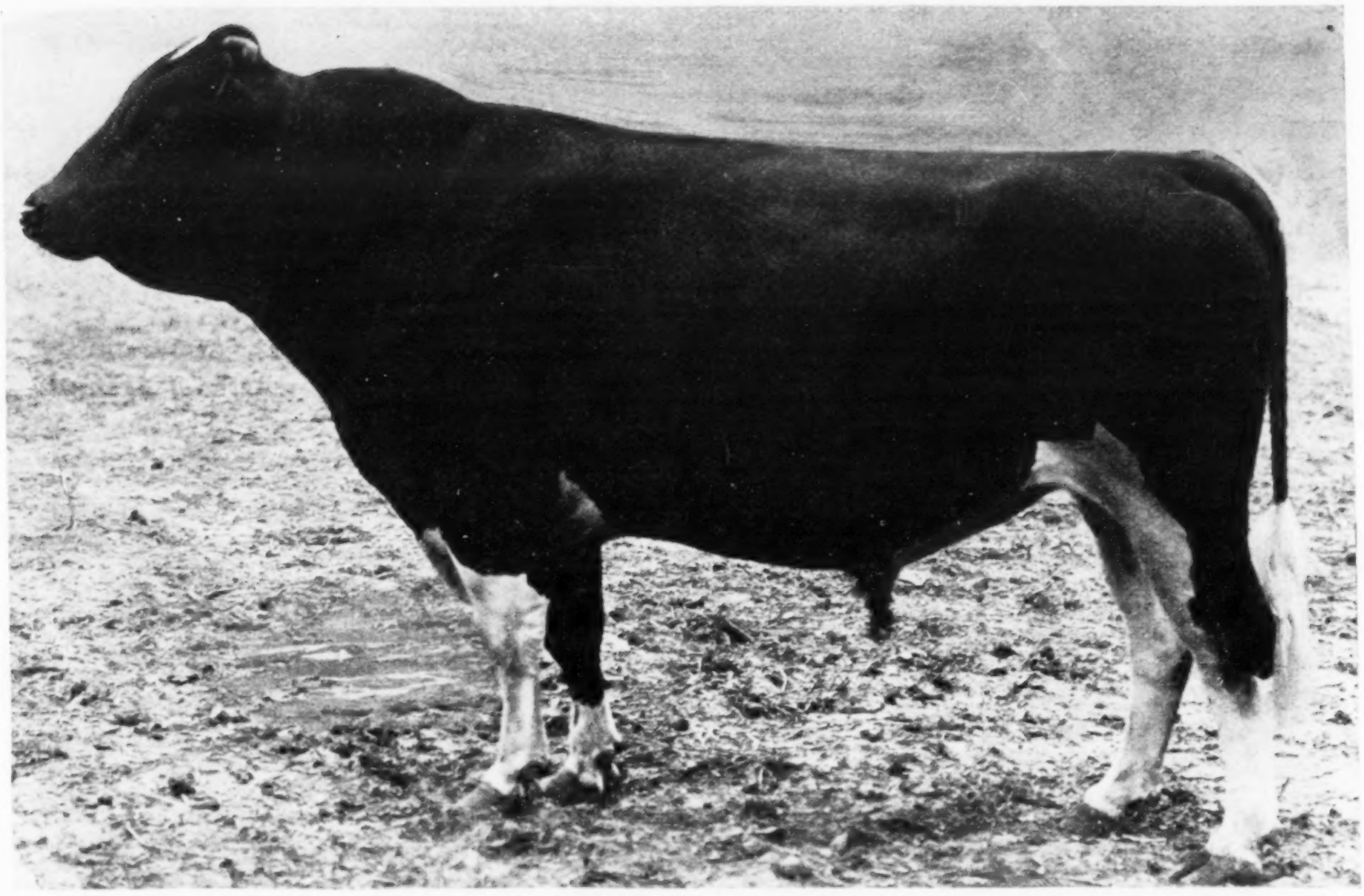
Analysis of Data

In order to simplify the treatment of the data, we first determined the correlation between the amounts of black on the two sides of the body for



OFFSPRING OF THE DARK BULL

FIGURE 19. By cows of all grades, having an average of 353 units of black, King Pietertje Ormsby Piebe produced calves having an average of 638 units of black. Most of the calves are distinctly dark, but the presence of lighter individuals indicates that the bull is heterozygous for spotting characters, and carries factors for the lighter grades of spotting, concealed by the dominant darker colors. This group of King Pietertje's offspring sold at an average of $5,030, a strong argument for raising pure-bred cattle. Photograph courtesy of Hargrove and Arnold, and the Holstein-Fresian World.



THE DARK BULL

FIGURE 20. King Pietertje Ormsby Piebe 16594 has 900 units of black and only about fifty units of white. This is probably the dominant type of spotting in Holstein cattle, although this animal is not genetically pure for his spotting characters (see Figure 19). He is the world's highest yearly record bull for both butter and milk production. Owned by Hargrove and Arnold, Norwalk, Iowa. Photograph courtesy of the Holstein-Fresian World.

all animals used.[2] This correlation was found to be very high ($r=.971 \pm .002$). There was almost perfect agreement between the amounts of black on the right and left sides indicating that we were probably dealing with a general variation of black pigment present and that a description of one side of the body could be used with almost perfect accuracy as a description of the total amount of black pigment in the whole coat. Thereafter we used only the amount of black pigment on the *left* side as the spotting grade of the animal.

We next determined the gross amount of variation in spotting for the whole series of 142 dams, since these were taken as a random sample of the breed. These cows ranged in amount of black from about grade 10 (about 1 per cent black) to about grade 925 (about 92 per cent black). The small amounts of black in the lowest grades were centered principally on the head and particularly about the eyes, while in the darkest grades the small amounts of white appeared on the lower legs and along the underline. The absence of the extremes of self white and self black is due to the requirement of the association that animals eligible for registry shall be black and white. The variation appeared to be symmetrical and continuous from the lightest to the darkest grades. The mean grade of this random sample of cows was 433 units (about 43 per cent black) or slightly less than the mean of the possible extremes (475 units). This is perhaps due to a sexual difference since it is in-

[2]In this correlation and wherever biometrical methods were used we grouped the individuals in classes of 50 units, viz.: 0-49 units of black; 50-99 units, etc.

dicated below that females are probably somewhat lighter on the average than the males. The standard deviation of amount of black was 265 units while the coefficient of variation was 61 per cent. It is evident then that the spotting of these cows is extremely variable.

We then compared the two sexes in amount of spotting, using the offspring group in which the number of males and females was equal. The mean of all males was found to be 555.4 ± 22.9 units, while the mean of all females was 388.0 ± 20.8. The difference in mean grade was 67.39 ± 30.86, or slightly greater than twice its probable error which can hardly be accepted as statistically significant. We believe, however, that in a larger sample the males would be found to average somewhat darker than the females, and that this sexual difference accounts for the fact that the random sample of dams was somewhat lighter than the mean.[3] This probable sexual difference does not affect the conclusions which follow, since these are based on averages of equal numbers of male and female offspring.

We next compared the mean grades of the offspring of the light, medium and dark bulls. The results of this comparison are given in Table 1. The most obvious fact shown by this table is that the offspring of the three bulls which differed considerably in darkness, themselves differ in darkness in the same way as their sires. The progeny of King Model (Figure 15), a very light bull, are much lighter on the average than the offspring of King Pieterje (Fig. 20), a very dark bull, although the dams of the two lots were of similar darkness. The light bull produced light calves; the medium bull produced calves of medium darkness and the dark bull produced dark calves. The amounts of influence of the various sires on their offspring cannot be measured accurately by this method, for the group of cows with which each bull was mated did not prove to be of the same mean grades, although the method of random choice was designed to avoid such differences. The most serious departure in this respect is in the cows mated to the medium bull, King of the Pontiacs, which proved to be 200 units (20%) darker than the cows mated to either the light or dark bull. All groups of females, however, fall within the medium class and the mean grades of their calves clearly show the influence of the sire and point to the heritability of differences in darkness.

Each male, however, differs in darkness from the average of the females with which he was mated. The calves produced are in each case intermediate in darkness between the sire and the average of the dams. The average grade of the calves is very near to the average between the sire and dam as shown by the following tabulation:

Spotting of Sire	*Light*	*Medium*	*Dark*
Av. Grade of Parents..	220	449	623
Av. Grade of Offspring	201	430	638

This might be taken as evidence of a purely blending type of inheritance in which dominance was absent, such as that which characterizes some cases of size inheritance. But mass statistics alone are inadequate to establish the mode of inheritance, since individual differences are extinguished by averaging and we know now that in-

[3]An interesting parallelism is thus established between the spotting of Holstein cattle and the piebald spotting of guinea pigs. Wright (*Proceedings National Academy of Sciences*, 6:321, 1920) found that the males of all the piebald stocks of guinea pigs which he had observed had about seven per cent more color than the females. In the preliminary figures given above the Holstein males are darker than the females by about the same amount. In both animals sex, as Wright has suggested, acts as a modifier for the colored and white pattern, which is inherited independently of sex. A comparison of spotting in the males and females of two inbred stocks of piebald mice reveals no significant sexual difference (unpublished data).

heritance is in general a matter of individual differences and separable traits. We may, however, conclude that the average *result* of crossing animals of different grades is the production of offspring whose *average grade* is intermediate between those of the parents. This is purely a statement of average facts and not an explanation of the inheritance.

We next attempted to determine the differences in the hereditary contributions of the different sires used by measuring the resemblance or correlation in spotting between individual calves and their dams for each progeny group separately. We reasoned that if the germ cells of the sire contained factors recessive to those of the dams then there should be a high degree of resemblance between dam and offspring, because the contribution of the sire should not be visible in his offspring. If, on the other hand, the sire contributed dominant factors, the resemblance between offspring and dams should be altered (correlation lowered) by the "interference" of the factors from the male. If there were no dominance, the contributions of sire and dam to the offspring should be of equal effect and variation in the dams should be accompanied to some extent by variation in the offspring, resulting in low correlation between dams and offspring. This reasoning we believe to be sound, but in our own case many practical difficulties stand in the way of a direct application of this method. Chief of these is the fact that for at least two of the sires used we cannot be certain that the germ cells produced are alike; we have no good evidence that they are homozygous. Another difficulty is the fact that all three sires were not bred to exactly the same types of cows. The cows to which the light and dark bulls were bred are roughly of similar darkness, but the cows to which the medium bull was bred were darker than the other two groups. The most profitable procedure is therefore to compare the degree of dam-offspring resemblance in the progenies of the light and the dark sires.

The dam-offspring correlations are given in the last column of Table 1. There proved to be a high correlation ($r = +.61$) between the dams and offspring of the light bull (King Model) indicating that the factors contributed by this male were probably recessive to those of the dam. If the coat patterns of the offspring were determined wholly by the heredity of the sire and dam, then the contribution of the light sire has much less visible effect on the coat character of the offspring than the contribution of the darker dams. This last assumption is, however, probably not justified since some nonheritable variation exists.

The correlation between dams and offspring of the dark bull, while undoubtedly significant, is only about half as great ($r = +.34$) as the correlation between dams and offspring of the light bull. The relative importance of dam and sire is here reversed, the dark male having the greater determinative effect, indicating dominance of the factors contributed by him.

There proved to be no correlation between the dams and the offspring of the medium bull indicating possibly equal determinative effect of the contributions of sire and dam. Because of the probable independent segregation of spotting factors taking place in this cross (see below) indicating a heterozygous genotype for the male and many of the females in these matings, and because of the difference in mean grade of the mated cows we prefer to draw no conclusions from this correlation.

Accepting this as partial evidence of the dominance of the darker over the lighter grades of spotting, we next attempted to determine whether there was any clear evidence of the segregation of factors affecting the amount of spotting. We divided all animals used into three groups, classifying as "light" those with from 0 to 249 units of black; as "dark" those with 700 to 949 units of black; and as "medium"

those with 250 to 699 units. These divisions were not wholly arbitrary since the division points appeared to be regions of somewhat lower frequency in the whole distribution. We then listed the results of all matings within and between these groups, and have arranged these data in Table 2.

The cross of light by light was found to give practically all light. The two medium animals recorded were in one case a very light medium (250 units of black) which might easily have been placed in the "light" group and in another case a medium (450 units) whose dam was a cow with broken spotted areas distributed over the whole surface of the coat. The actual amount of black on this cow was 200 units left and 250 units right. Because of the extended distribution of spotting she might have been placed in the medium class. We should make no great misstatement in saying that the lighter grades of spotting breed true to this condition.

The cross of light and dark animals produced principally animals of medium grade with a few light and a few dark offspring. On the hypothesis of the partial dominance of dark the appearance of light animals would indicate that some of the darks, including the dark bull, were heterozygous. The appearance of some dark offspring indicates that the dominance of dark may be nearly complete. Medium animals bred together produced principally medium calves with some evidence of the segregation of light and dark animals. Medium females bred to light males produced a preponderance of light calves and some mediums but no darks, while the medium male bred to light cows produced in addition two dark calves. Medium by dark produced principally darks and mediums with distinct evidence of segregation of some lights. Dark by dark produced few calves of which four were dark and one was medium. A general survey of the individual matings showed that with few exceptions the calves produced were generally no darker than the darker of the parents, making the case somewhat analogous to the inheritance of shades of eye color in man. The exceptions were the dark calves produced by the medium bull when bred to both light and medium cows. It is possible that the medium bull was of a dark genotype, although he was phenotypically medium. Certainly he bred more like a dark than a medium bull. In general then it appears that the light animals used were fairly pure for this condition, while both the medium and dark bulls were heterozygous. The results of reciprocal crosses were not always similar, there being usually an excess of dark animals in the offspring of the dark and medium bulls; the males appeared more "prepotent" in transmitting darkness. But with this small sample of animals tested no conclusions from this are warranted. The chief result of the evidence considered in this way is the demonstration of the segregation of the lighter from the darker grades, without the reverse phenomenon except in the case of the phenotypically medium bull.

Non-Genetic Variation

We have no good evidence on the amount of non-genetic variation in these spotting patterns, but it probably occurs to a degree. The best measure of it would be the amount of variation existing in identical twins; and we have been unable so far to assemble indisputable cases of identical twinning.

The recent data of Gowen[4] and of Lillie[5] indicate quite conclusively that identical twinning in cattle is extremely rare, if it does occur. Lillie finds in his Keller's and Tandler's cases (p. 52) only one certain case of identical twinning out of 126 cases of monosexual twins in which the number of corpora lutea in both ovaries

[4] Gowen, J. W. *Biological Bulletin* 41: 1-6. 1922.
[5] Lillie, F. R. *Ibid.*, 44:47-78. 1923.

OFFSPRING OF KING PIETERTJE

FIGURE 21. Notice how closely the calves resemble their sire, not only in amount of black and white, but in its distribution. A certain amount of non-genetic variation certainly occurs, but just how much is difficult to determine. Photograph courtesy the Holstein-Fresian World.

could be determined. Because of the tendency of originally separate chorions to fuse, the evidence from the conditions of the membranes at birth is not reliable, so that this method which would seem to offer a mode of attack on the problem of spotting inheritance, appears actually to be of no value. Gowen (loc. lit.) collected 1122 cases of twins in Jersey cattle and from the degree of resemblance in body markings between monosexual as compared with bi-sexual twins and sisters of separate births concluded (p. 5), "These facts all point to not more than a low percentage of identical twins in cattle if they exist at all."

Of the two pairs of monosexual twins in our series, one pair is alike in coat pattern, one member having

250 units of black left
150 units of black right

and the other

150 left
150 right

The members of the other pair are dissimilar, one being

200 left
100 right

the other

650 left
650 right

The second pair is from a cross of light by dark and shows segregation of light and medium; while the first pair is from medium by light and shows segregation of light from medium. In view of the facts cited above, the resemblances and differences of these twins are only such as might be expected to arise from segregation of spotting factors in individuals of separate birth.

Discussion and Conclusion

The results obtained from this study are chiefly of value in pointing out an interesting problem for which a greater amount of material is available than for any other problem of coat color or spotting inheritance known to us, and in indicating some of the methods by which it may be attacked.

The preliminary evidence is sufficient to indicate that:

(1) Differences in amounts of spotting in Holstein cattle are inherited, and amenable to selection even when this is practised on the male side only as in the present case.

(2) That the darker grades are probably partially dominant over the lighter grades.

(3) That segregation of factors determining the grosser difference in spotting occurs.

(4) That some degree of blending occurs, due possibly to minor modifying factors whose expression together with that of the major factor or factors may be obscured by non-genetic variation at present not measured.

(5) Because of the extreme rarity of proven cases of identical twinning in cattle it will probably not be possible to measure the amount of this non-genetic variability by the comparison of the spotting patterns of monosexual twins.

The present data cannot be used for measuring the number or the quantitive effects of the factors involved since in the absence of knowledge concerning the genotypes of the animals used, the proportions of offspring of various types can have little significance. There is every indication, however, that an exact interpretation can be arrived at through the collection and study of more data.

TABLE 1. *Average results of crossing bulls of different spotting grades with females of all grades*

Sire			*Mean Grade Units of Black*	*Standard Deviation (Units)*	*Coefficient of Variation (Percent)*	*Coefficient of Correlation Dams and Offspring*
King Model	Dams	46	392.39± 24.91	250.50± 17.62	63.84± 6.05	.61± 06
(Light, grade 50)	Offspring	50	201.00± 15.41	161.50± 10.89	80.35± 8.24	r/Er = 10.16
King of the Pontiacs	Dams	49	549.49± 24.38	253.00± 17.24	46.04± 3.74	.05± .10
(Medium, grade 359)	Offspring	49	430.10± 23.32	242.00± 16.49	46.27± 4.90	r/Er = .50
King Pietertje Ormsby Piebe	Dams	47	353.73± 24.50	249.00± 17.32	70.39± 6.91	.34± .08
(Dark, grade 909)	Offspring	50	638.00± 23.66	248.00± 16.73	38.87± 2.99	r/Er = 4.25
All Dams		142	433.80± 14.20	265.00± 10.61	61.09± 3.23	

TABLE 2. *Results of crosses among Holstein cattle of various grades of spotting.*

Parents	*Offspring*			
	Light (0-249)	*Medium* (250-699)	*Dark* (700-949)	*Mean Grade Offspring*
Light ♂ × Light ♀	13	2	—	125.00 ± 81.68
Light ♂ × Dark ♀	1	7	—	431.25 ± 31.24
Light ♀ × Dark ♂	3	12	6	555.95 ± 33.85
Medium ♀ × Medium ♂	6	13	2	457.86 ± 32.38
Medium ♀ × Light ♂	20	7	—	175.00 ± 15.77
Medium ♂ × Light ♀	3	5	2	370.00 ± 50.98
Medium ♀ × Dark ♂	3	7	14	677.09 ± 34.21
Medium ♂ × Dark ♀	2	10	6	566.67 ± 37.12
Dark ♂ × Dark ♀	—	1	4	795.00 ± 56.11
Total	51	64	34	149